Palaeoecology of Fossil Mammal Assemblages from Some Australian Caves

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Abstract: The paper presents an analysis of a subfossil deposit from Pyramids Cave, eastern Victoria, and a reassessment of the Broom fauna of Wombeyan Caves, New South Wales. To provide a basis for the analysis, assessment is made of the habitat of each of 30 species of murids and small marsupials which have been recorded, living or fossil, from within 100 miles of the site. Details are given of the form of the cave, the disposition of the bone deposit found in it, and of the local geology, topography and vegetational formations. Data are presented of numbers and percentages of each mammal species (a) in each of two fractions of the deposit (identified as Holocene and late Pleistocene in age), and (b) in each of several categories of the Pleistocene fraction.

Inferences are drawn regarding changes in vegetation during the period of accumulation of the deposit, and the sequence is related to climatic change during the past 20,000 years. Comparisons are made between cranial measurements of mammal series from the two fractions of the deposit and further, with modern museum series. Data are given of fossil specimens from the Broom deposit, Wombeyan Caves, New South Wales, novelties described from that collection are examined, several lectotypes are nominated, and synonymies with extant species are indicated. The Broom deposit is compared with the Pyramids Cave deposit and an assessment made of the age of the Broom fossil fauna.

INTRODUCTION

Initially the interest in this study centred round the discovery, near Buchan in eastern Victoria, in what is now known as the Pyramids Cave, of a deposit of mammal bones containing specimens of *Burramys*, which was known otherwise only from fossil bone breccia from Wombeyan Caves in eastern New South Wales.

In discussing the Wombeyan Caves fossil fauna, Ride (1960) noted that insufficient was known of modern ecological relationships and of basic taxonomy of Australian mammals for valid comparisons of faunal assemblages and palaeoecological interpretations to be made. The research reported here has endeavoured to provide some of the necessary foundation for such work in south-eastern Australia, and has therefore included field studies of habitat and distribution of mammals, taxonomic revision, and quantitative analyses of fossil deposits from various localities.

In previous reports (Wakefield 1960a, 1960b) the Pyramids deposit was shown to consist essentially of pellet material regurgitated by owls of the genus *Tyto*, probably *T. novae-hollandiae*. Two groups of bones were recognized: one hard whitish (unaltered) bones, the other bones which had become fragile in texture and reddish in colour. These two groups are referred to respectively as the whitish fraction and the reddish fraction of the deposit, and they are eventually identified as Holocene and Pleistocene in age. The term 'modern' is applied to the period of occupancy of Australia by Europeans.

Species names in this paper are according to the taxonomy adopted by Ride (1970), but the family Phalangeridae is here used in the earlier broad sense to include such genera as *Petaurus* and *Burramys*.

Locality and rainfall data are set out in Table 4. Locations of bone deposits are shown in Fig. 1.

Institutions are abbreviated thus: AM (Australian Museum, Sydney); BM (British Museum, Natural History, London); FWD (Fisheries and Wildlife Department, Melbourne); NMV (National Museum of Victoria, Melbourne); SAM (South Australian Museum, Adelaide).

HABITAT DATA OF MARSUPIALS AND MURIDS

This section deals with all native murids and

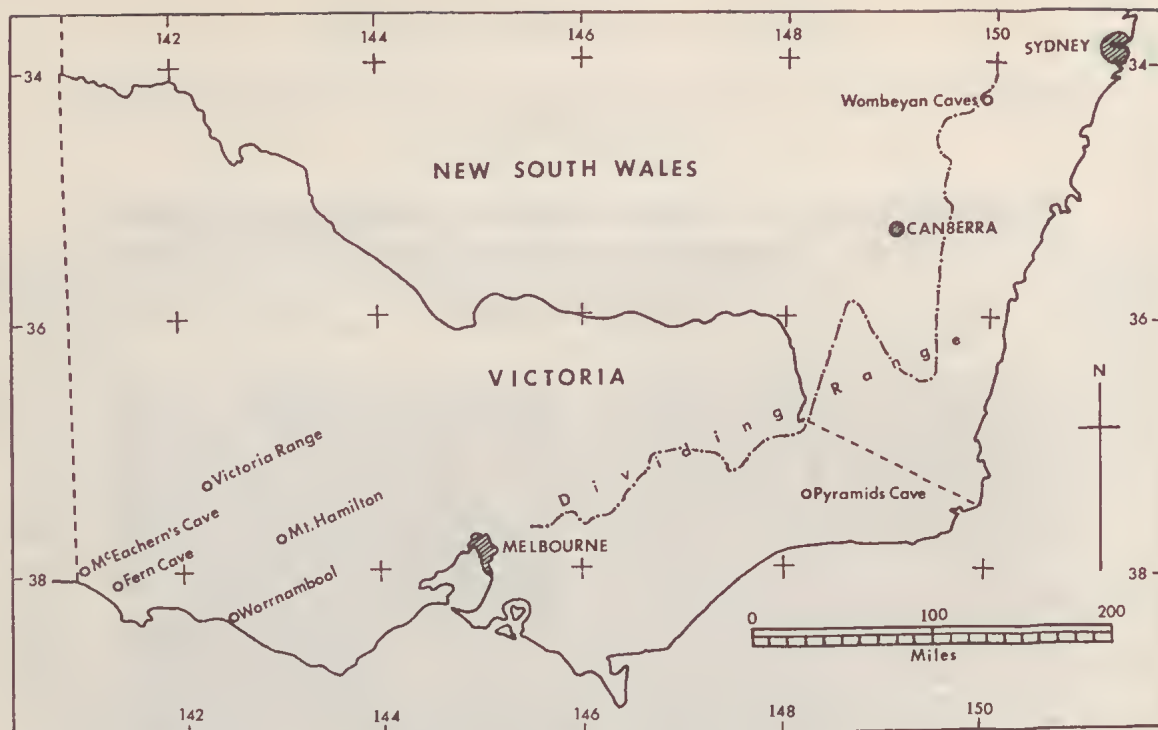* Biology Department, Monash Teachers' College, Clayton, Victoria 3168.

FIG. 1—Localities of fossil deposits.

small to medium-sized marsupials which are re-corded, living or fossil, from the south-eastern side of the Dividing Range and within 100 miles of Pyramids Cave (Fig. 1).

For most marsupials the habitat classification of Marlow (1958) is given first. In other cases the more pertinent data of other authors are used. Marlow's habitat assessments refer to general vegetational formations of regions in which species are recorded, rather than to specific habitats, and he does not differentiate between wet and dry sclerophyll forests.

When relevant to assessment of habitat, selected museum specimens are cited next. Unless other-wise indicated, specimen numbers in this section apply to registrations in the NMV.

The data are then discussed, and note is made, in parenthesis, of the nearest modern record to the Pyramids site.

For most species, assessment of habitat follows. These assessments apply to south-eastern Australia and do not necessarily apply to habitat preferences or tolerances in other Australian regions and in different faunal assemblages.

Estimates of the range of mean annual rainfall (M.A.R.) are appended to the assessments. These are based mainly on data shown in Table 4, and the figures, given in inches, are rounded to mul-tiples of 5. In some cases the figures refer actually to total precipitation, including snow. While noting rainfall, it is remarked that habitats tend to be wetter at high elevations and drier on slopes of northerly aspect, due to effects of temperature on evapotranspiration and hence on ground moisture.

In assessing habitat, use is made of information gathered from extensive observational and trap-ping experience during the past 15 years, and of first-hand knowledge, accumulated over 34 years, of vegetational characteristics in most regions of Victoria. In a number of cases, such information has indicated that certain specimens may have originated some distance from the actual town for which they are recorded, and this is borne in mind when framing assessments.

DASYURIDAE
Sminthopsis leucopus
Marlow (1958): Sclerophyll forest.
SPECIMENS: Portland area (C2, C1023-4), Beech Forest (C891-2, C925), Waratah Bay (FWD, D523-5, D741).
DISCUSSION: Portland and Waratah Bay areas carry dry sclerophyll forest, and the Beech Forest area is mixed wet and dry forest. No evidence is available of the species occurring in wet forest. (FWD, D498; The Basin, 4 miles E. of Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Dry sclerophyll forest, including areas near wet forest. M.A.R., 30-65 in.

Antechinus stuartii

Habitat is discussed by Wakefield and Warneke (1967). (FWD, DY8-9; Pyramids area, in wet vegetation.)

ASSESSMENT: Abundant in wet sclerophyll forest, less so in dry forest. M.A.R., 20-75 in.

Antechinus swainsonii

Habitat is discussed by Wakefield and Warneke (1963). (FWD, D509; W Tree, 7 miles N. of Pyramids, in wet tussocky gully.)

ASSESSMENT: Predominantly wet sclerophyll forest, but also wet microhabitats in dry forest areas. M.A.R., 35-95 in.

Phascogale tapoatafa

Marlow (1958): Rainforest, sclerophyll forest, woodland.

SPECIMENS: Brit Brit (C2475, C3135), Casterton (C2655), Cavendish (C4262), Marysville (C6878), Healesville (C1443).

DISCUSSION: Most specimens are from woodland and dry forest areas. Several are from areas of mixed wet and dry sclerophyll forest. No evidence is available of occurrence in wet sclerophyll forest. (C7887; Gelantipy, 23 miles N. of Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Woodland and dry sclerophyll forest, including areas near wet forest. M.A.R., 20-50 in.

Dasyurus viverrinus

Marlow (1958): Uncommon in sclerophyll forest, rare in woodland.

SPECIMENS: Kew (C6058-80), Bacchus Marsh (C6081).

DISCUSSION: According to Troughton (1941) the species was decimated by an epidemic disease in 1901-3 and disappeared over a great part of its known range. No museum specimen is available from eastern Victoria or southern New South Wales. However, Wakefield (1954) states that it was abundant in the Bairnsdale area (eastern Victoria) prior to its disappearance about 1902, and Buckland (1954) records a similar history for the Delegate area (southern New South Wales). The species had lairs in the Pyramids area (Wakefield 1960a, 1960b).

ASSESSMENT: Dry sclerophyll forest and woodland, favouring more open areas and broken rocky country. M.A.R., 20-35 in.

PERAMELIDAE

Perameles nasuta

Marlow (1958): Abundant in rainforest, common in sclerophyll forest, uncommon in woodland.

SPECIMENS: Narracan (C7012-3, C7055, C7190, C7203), Gellibrand River (C7494, C7770), Tolmie Ranges (C7209-11).

DISCUSSION: The Victorian range is mainly in and about wet forests of the central and eastern highlands, south-eastern Victoria and the Otway Ranges, with some dry forest records from eastern Victoria. (C2129-31; Head of Basin Creek, 6 miles NE. of Pyramids, in wet forest; and diggings seen in Pyramids area are attributed to the species.)

ASSESSMENT: Mainly wet sclerophyll forest but also in comparatively wet parts of dry sclerophyll forest. M.A.R., 30-75 in.

Isoodon obesulus

Marlow's (1958) classification of habitat is based mainly on (a) specimens from eastern New South Wales now identified in AM collections as *I. macrourus* and (b) specimens from Murray-Darling Junction area regarded by Wakefield (1966) as distinct from the *I. obesulus* of southern Victoria.

SPECIMENS: Portland (C697-9, C714-5), Halls Gap (C7529), Yellingbo (C7056).

DISCUSSION: The Victorian range is mainly near-coastal, in areas with soft soil and dense shrubbery or tussocks. The southern Victorian form is not recorded from Pleistocene deposits and may have crossed from Tasmania during the last glacial period. (FWD, B98; 12 miles W. of Orbost, 21 miles S. of Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Dry sclerophyll forest and heathland, including areas near wet forest. M.A.R., 30-40 in.

PHALANGERIDAE

Acrobates pygmaeus

Marlow (1958): Sclerophyll forest and woodland.

SPECIMENS: Mount Dandenong (C783-4, C3993-4), near Bendock (FWD, F222), Gorae Forest (C5068-70), Ouyen (C4013), Nangiloc (C5937).

DISCUSSION: The Victorian range is from the northern Mallee to southern and eastern Victoria. Most records are from high rainfall areas. No evidence is available of the species inhabiting open woodland. (C1436; W Tree, 7 miles N. of Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Predominantly wet sclerophyll forest and dry forest areas of medium to high rainfall, less common in drier formations. M.A.R., 10-75 in.

Cercartetus nanus

Distribution and habitat are discussed by Wakefield (1963a). (FWD, P230, Nowa Nowa, 19 miles SSW. of Pyramids, in dry forest.)

ASSESSMENT: Dry sclerophyll forest, especially in scrubby near-coastal formations; uncommon in mountain areas of high rainfall. M.A.R., 20-50 in.

Cercartetus lepidus

The species is known on the Australian mainland only from Pleistocene fossils. The few habitat data of the extant Tasmanian population are discussed by Wakefield (1963a). A specimen (SAM, M6338) is reported

from Kangaroo Island, S. Aust. (Aitken 1967), but it is doubtful that the species is indigenous there (Wakefield 1970a).

ASSESSMENT: Probably associated on mainland Australia with wet sclerophyll forest areas.

Burramys parvus

Dixon (1971) discusses the habitat of a specimen collected near Falls Creek, Bogong High Plains, Victoria.

SPECIMENS: Mt. Hotham (C7290), Falls Creek area (C10112).

DISCUSSION: All specimens to date are from about 5,000 to 6,000 ft elevation, in localities subject to heavy winter snow drifts. (Mt. Hotham is 60 miles NW. of Pyramids.)

ASSESSMENT: High montane shrubbery and scattered *Eucalyptus pauciflora*. Mean annual precipitation, 50-95 in.

Gymnobelideus leadbeateri

SPECIMENS: Bass River (C4280), 6 miles E. of Marysville (C6193), Tanjil Bren (FWD, P638).

DISCUSSION: All records of unquestionable locality data are from high rainfall areas carrying *Eucalyptus regnans, E. nitens* or *E. delegatensis*. (C4377; Sunnyside, 50 miles NW. of Pyramids, in wet forest.)

ASSESSMENT: Wet sclerophyll forest. M.A.R., 40-75 in.

Petaurus breviceps

Marlow (1958): Common in sclerophyll forest, uncommon in woodland.

SPECIMENS: Kallista (C2863), Ferny Creek (C3699), Victoria Valley Road, Grampians (C3006-7).

DISCUSSION: Recorded near Kaniva (Wakefield 1966). There is no specific evidence that the species inhabits open woodland, and it apparently requires close formations approaching sclerophyll forest. (Observed by spotlight near Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Abundant in wet sclerophyll forest, less so in dry forest, occasionally in comparatively close woodland. M.A.R., 20-75 in.

Petaurus norfolcensis

Marlow (1958): Uncommon in sclerophyll forest, rare in woodland.

SPECIMENS: Near Colbinabbin (FWD, P203), Dadswells Bridge (FWD, P506, P703), Warrenbayne (FWD, P660, P685), between Shepparton and Mooroopna (FWD, P635).

DISCUSSION: Except for an old specimen of doubtful origin (NMV, 'Western Port'), all modern Victorian specimens are from open woodland formations with *Eucalyptus microcarpa* dominant. (Marlow cites a specimen from Bega, N.S.W., 110 miles NE. of Pyramids.)

ASSESSMENT: Woodland. M.A.R., 20-35 in.

Petaurus australis

Habitat is discussed by Wakefield (1970b). (Evidence of feeding observed near Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Wet sclerophyll forest (but not in *Eucalyptus regnans* stands), and dry sclerophyll forest, including riparian corridors in woodlands. M.A.R., 20-97 in.

Pseudocheirus peregrinus

Marlow (1958): Common in rainforests, sclerophyll forests and woodland.

SPECIMENS: Near Warburton (C3903-12), Cashmore (C1495-501).

DISCUSSION: These two series are from wet and dry forest areas respectively. Many concentrations have been noted in wet forests. The species is plentiful in open woodland near Dadswells Bridge. (Observed by spotlight near Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Abundant in both wet and dry sclerophyll forest, plentiful in some woodlands. M.A.R., 20-75 in.

Schoinobates volans

Marlow (1958): Abundant in sclerophyll forest, uncommon in woodland.

SPECIMENS: Healesville (FWD, P259, P636), 6 miles E. of Marysville (C7242).

DISCUSSION: Victorian distribution is limited to tall forests of central and eastern mountain areas, where population is dense. No specific evidence is available of occurrences in typical dry sclerophyll forest or woodland. (C2132, C2136-8; Head of Basin Creek, 6 miles NE. of Pyramids, in wet forest.)

ASSESSMENT: Abundant in wet sclerophyll forest, less abundant in wetter parts of dry sclerophyll forest. M.A.R., 40-70 in.

MACROPODIDAE

Bettongia gaimardi

Distribution of the now-extinct mainland Australian race is discussed by Wakefield (1967a), but no precise data of Victorian habitat are available. Remains occurred in an owl pellet deposit in the Victoria Range, western Victoria (Wakefield 1963b). For eastern Victoria there is no record as a living modern animal or as prey of owls, but remains of recent age were found in dens of *Dasyurus* in the Pyramids area (Wakefield 1960a).

Potorous tridactylus

Marlow (1958): Rare in rainforest, sclerophyll forest and woodland.

SPECIMEN: 'Muddy Creek ranges' (C6973).

DISCUSSION: It is probable that C6973 originated about Toolangi, near the upper Yea River, of which Muddy Creek is a synonym. (The collector, F. J. Williams, secured other specimens from neighbouring localities in the same region.) (FWD, MT1878; Yalmy River, 18 miles ENE. of Pyramids, at 2,000 ft elevation.)

ASSESSMENT: Wet sclerophyll forest. M.A.R., 40-50 in.

Potorous apicalis

SPECIMENS: Heathmere (FWD, MT531, MT533, MT638-9), Forrest (FWD, MT1201, MT1204-5, MT1207), Pomonal (FWD, MT1241-2, MT1964-5), French Island (FWD, MT1883, MT1887-99).

DISCUSSION: Victorian distribution is lowland and mainly near-coastal, and dense ground cover is required. (FWD, MT1884; Bete Bolong, 19 miles SSE. of Pyramids, in dry sclerophyll forest.)

ASSESSMENT: Scrubs in areas of wet and dry sclerophyll forests. M.A.R., 30-45 in.

MURIDAE

Hydromys chrysogaster

DISCUSSION: Ubiquitous in lakes and estuaries and in streams to moderate elevations. (Reported in Murrindal River, 4 miles N. of Pyramids (J. Hodge, pers. comm.).)

ASSESSMENT: In and about waterways irrespective of vegetational formation and rainfall.

Rattus fuscipes assimilis

Calaby (1966): 'Common in rainforest, wet well-vegetated gullies, and along creeks with shrubby vegetation on the banks. It was not found in other situations.'

SPECIMENS: Very large series from Beech Forest (NMV) and Loch Valley (FWD), smaller series from numerous other localities in central and eastern Victoria.

DISCUSSION: Densest populations occur in areas of highest rainfall, in lowland wet sclerophyll forests and in grass and scrub along montane streams. Populations are proportionately less dense in less wet areas. There is no evidence of occurrences in lowland grassland or woodland. (FWD, R1222-3; near Pyramids, in dense vegetation on wet terrain.)

ASSESSMENT: Most abundant in wet sclerophyll forest, less so in comparatively wet situations in dry forest areas. M.A.R., 30-95 in.

Rattus lutreolus

Calaby (1966): 'In long grass along creek banks . . . also in areas of undisturbed long grass in wet hollows in woodlands on higher ground, including wet shelves on hillsides.'

SPECIMENS: Hordern Vale (C392-6, C398-401, C403-17), Portland (C4899, C5490), Grampians (C7343), Stoneyford (C7716, C7766-7).

DISCUSSION: Mainly near-coastal and sometimes sympatric with R. fuscipes, but appears to be the less vigorous and does not extend far into the other's habitats. It extends into the basalt plains and Grampians of western Victoria, where R. fuscipes is absent. (Observed near Orbost, 22 miles SE. of Pyramids, on deeply grassed alluvial flats.)

ASSESSMENT: On more-or-less flat, well grassed, wet terrain in lowland areas of wet and dry sclerophyll forest, woodland and grassland. M.A.R., 25-55 in.

Pseudomys oralis

The sole living specimen was obtained from Hastings River, north-eastern New South Wales, and no habitat data are recorded.

Pseudomys higginsi

Green (1968): From near sea level to about 3,000 ft, in or near rainforests. M.A.R., about 50-100 in.

DISCUSSION: This assessment applies to the extant Tasmanian race, and it may not be applicable to the extinct mainland Australian race, which is known only from Pleistocene fossils.

ASSESSMENT: The Australian P. higginsi probably favoured wet forest areas, but precise habitat is unknown.

Pseudomys fumeus

Brazenor (1934): 'Forest country with thick undergrowth of scrub which is literally riddled with runs of Rattus assimilis.'

SPECIMENS: Near Beech Forest (C197, M853), Silverband Falls (FWD, R2430-1, R2438-9), Upper Thomson River (FWD, 5837).

DISCUSSION: The Silverband Falls occurrence is in a wet sclerophyll forest microhabitat in a dry forest region. Only a few relict populations are known, and the species may have had a less restricted range of habitat formerly. (Upper Thomson River is 110 miles W. of Pyramids.)

ASSESSMENT: Wet sclerophyll forest, including microhabitats in comparatively dry areas. M.A.R., 35-75 in. Possibly tolerant of lower rainfall.

Pseudomys novaehollandiae

Keith and Calaby (1968) summarize the habitat of a relict colony in north-eastern New South Wales as lowland dry sclerophyll forest with shrubbery and bracken but little grass; M.A.R., 25-53 in.

SPECIMENS: Tyabb (C9578-9; FWD, 5098, 5126-7); Seacombe, 22 miles SSW. of Bairnsdale (C10346-10).

DISCUSSION: The three known relict populations are near-coastal. In the cooler Victorian latitudes a M.A.R. limit somewhat below 53 in. may be assumed. Some early Australian specimens which reached the BM under the name P. novaehollandiae prove to be Mus musculus (J. A. Mahoney, pers. comm.), so the habitat data of Troughton (1941) may contain error. (Seacombe is 65 miles SW. of Pyramids.)

ASSESSMENT: Dry sclerophyll forest. M.A.R. 25-45 in.

Melomys cervinipes

J. H. Calaby (letter, 3 July 1970) states that the species is found in 'rainforest but also in medium-wet sclerophyll forest' in south-eastern Queensland, and that the type locality, Stradbroke Island, does not carry rainforest.

DISCUSSION: The late Pleistocene subfossils from Pyramids Cave comprise the sole southern Australian record of the species (Mahoney 1965).

ASSESSMENT: Rainforest and wet sclerophyll forest, but evidently with wider tolerance.

Mastacomys fuscus

Green (1968) found that the Tasmanian *M. fuscus* is invariably 'within the vicinity of the drainage systems' of 'wet sedgelands which occur as forest openings'. Calaby and Wimbush (1964) summarize data of distribution and habitat of the Australian mainland populations.

DISCUSSION: With the exception of a predator-killed specimen (C8146) picked up near Leongatha, modern mainland specimens are all from high rainfall areas. However, these represent relict populations, and the species may have occurred formerly in areas of lower rainfall. There is no evidence of occurrence in dense forest, and Green's findings appear to be applicable to Australia also, except that dense growths of grass (*Poa*) may provide cover instead of sedges. (FWD, R3116; Dargo River headwaters, Mt. St. Bernard, 60 miles NW. of Pyramids, by runnel bordered by *Carex* in wet forest area.)

ASSESSMENT: Very wet open areas with low dense vegetational cover, in areas of wet sclerophyll forest, but probably also tolerant of wet terrain with grass/sedge coverage in other vegetational formations. M.A.R., 35-95 in.

Conilurus albipes

Troughton (1941): 'Widely inland wherever there was tree-growth.'

DISCUSSION: The sole modern Victorian record is an observation in the Broadford area in 1839, recorded by Parris (1950).

ASSESSMENT: Woodland. M.A.R., 20-35 in.

None of the three murids—*Pseudomys fumeus, P. oralis* and *Conilurus albipes*—has been recorded as a living animal within 100 miles of the Pyramids. The first survives as scattered relict populations (see p. 5) and the other two are presumably extinct. However, subfossil remains indicate that these three, and *Mastacomys fuscus* as well, were each plentiful in the Buchan (and Pyramids) district until very recently, probably until about 100 years ago. The widespread disappearance of populations of these and other pseudomyine murids in SE. Australia, evidently soon after European settlement, suggests an epidemic of the kind thought to have decimated *Dasyurus viverrinus*.

Of the 30 species dealt with in this section, only the two largest, *Bettongia gaimardi* and *Potorous tridactylus*, were not found in the Pyramids Cave deposit. With the addition of 10 species of bat (see Table 1) to the 18 marsupials and 10 murids, the total number of mammals caught by the Pyramids owls stands at 38 species.

PYRAMIDS CAVE

ENVIRONMENT

Pyramids Cave is approximately 500 ft above sea level, in the lower part of a north-south cliff some 45 ft high, and half way down the steep easterly slope of a hill capped by the residuals known as the Pyramids, 4 miles NNE. of Buchan, eastern Victoria. The hill is part of the Buchan Caves Limestone formation, of Middle Devonian age (Teichert and Talent 1958), but this gives place, about 200 ft down from the cave, to an extensive tract of acid rock of the Snowy River Volcanics, into which, at the foot of the Pyramids hill, the Murrindal River has cut a minor gorge.

The cave has an open outer chamber, approximately 7 ft long, 7 ft high, and from 1 to 3 ft wide, with its outer lower lip 12 ft above the base of the cliff. Inward from the lip, the floor slopes downward, and about one-third of the deposit of bones was collected from this outer chamber. A ledge against the south wall of the chamber served as a landing platform and pathway, and a slightly higher ledge at the rear provided a roost, for the owls that sheltered in the chamber. (Pl. 1.)

At the base of the rear of the outer chamber, a small opening led to an inner chamber, and during excavation a second, larger, aperture was revealed, underneath the first. The inner chamber comprised a trough 7 ft long and averaging 1 ft wide, filled to a depth of 2 ft with the bulk of the bone deposit, and then a vertical chimney 12 ft deep and several feet in diameter. The trough lay between the two apertures and the upper part of the chimney. From the lower end of the chimney, a horizontal tunnel, about 1 ft wide, 2 ft high, and 10 ft long, led out to the base of the cliff.

The features described comprise the complete cave system, and there is no aperture or crevice anywhere to provide possible connection to any further chamber or tunnel. It is obvious, from the form of the cave system, that, except for the few mammals which may have used the cave as a home, and died there, the deposit was a predator-den accumulation which originated in the outer chamber. Gravitational movement, possibly assisted at times by passage of animals to and fro in the cave, would have been responsible for the entry of material into the inner chamber. Possums (*Trichosurus*) had a nest in a recess near the roof of the inner chamber, and residents of this kind may sometimes have maintained their access by scraping back, into the inner chamber, material accumulated in the outer chamber.

The remarkable state of preservation of the deposit, as clean, free bones, appears to have been due to (a) the eastern aspect of the cliff and a considerable overhang above the cave, which protected the system from prevailing westerly weather, (b) the movement of accumulated

material further back into the system, (c) the desiccating action of the limestone dust with which the bones were mixed, and (d) the evident complete absence of water flow into or through the deposit at any stage.

The following material, which did not originate there as prey of owls, was also in the deposit:

A. Cranial and post-cranial bones of a single *Trichosurus*, not specifically identified, which evidently died in the cave.

B. A mummified adult and the remains of several juvenile specimens of *Antechinus stuartii*, which also appear to have died in the cave.

C. A single I_3, but no other recognizable bones, of *Sarcophilus laniarius*.

D. A quantity of small fragments of large mammal limb-bones.

E. Two incisors and a molar, comparable with those of *Petrogale penicillata*.

Items C, D and E are of the reddish colour of the older fraction of the deposit, and they indicate that the outer chamber was at some stage used as a den of *Sarcophilus*. The macropodid teeth and fragments of limb-bones would represent defaecated remains of this carnivore's food. (See Pl. 1, fig. 3.) Douglas, Kendrick and Merrilees (1966) identify similar fragments, from a cave deposit in Western Australia, as faecal residue of *Sarcophilus*. The entry of this predator into the outer chamber of the Pyramids Cave would require the talus to have been ten feet higher than at present, and that usage would have pre-dated occupancy by owls.

The acid rock formation from the Murrindal River eastward carries dry sclerophyll forest, with *Eucalyptus macrorhyncha, E. globoidea, E. sideroxylon* and *E. polyanthemos* the main trees. Smaller trees and shrubs include *Acacia melanoxylon, A. mearnsii* and *A. botrycephala*. Along Shaws Creek (a tributary of the river) in the same area, there is a minor element of wet sclerophyll forest vegetation, with shrubs such as *Pomaderris aspera, Olearia phlogopappa, O. argophylla, Lomatia myricoides* and *Correa lawrenciana*. In places along the Murrindal River there are minor elements of warm-temperate rainforest vegetation, with the tree *Tristania laurina* and lianas such as *Tylophora barbata, Eustrephus latifolius* and *Smilax australis*.

The limestone areas about the cave and the Pyramids hill are open woodland dominated by *Eucalyptus melliodora*, with *Casuarina stricta, Acacia implexa* and *Brachychiton populneus*. About the cliffs and steep rocky slopes, *Pittosporum undulatum* and the liana *Marsdenia rostrata*

are abundant, these being typical units of warm-temperate rainforest. There are small rocky ravines in the top of the Pyramids hill, with abundant ferns and other soft-leaved vegetation.

Before it was cleared and extensively grazed, the Buchan limestone area would have comprised an extensive grassy woodland, more or less shrubby on the steeper rocky slopes, wet and deeply grassed in the hollows, and swampy on the alluvial flats.

Mean annual rainfall at the Pyramids would probably be slightly more than at Buchan, and it is therefore estimated at 33 in.

ANALYSIS OF THE DEPOSIT

During the excavation, record was kept of the level and area from which each bag of material was obtained. When it became apparent that the two texture/colour fractions represented two different faunal assemblages which had been separated in time (see below), and that each bag contained a mixture of bones of each fraction, it was concluded that the deposit had been mechanically mixed. It was therefore necessary to abandon the consideration of stratification as the primary factor in the analysis.

THE TWO FRACTIONS OF THE DEPOSIT

It had been suggested (Wakefield 1960b) that the reddish fraction of the deposit was older than the whitish fraction, and subsequent observations tended to confirm this. The basic evidence is as follows:

1. Except for the case of one incomplete skull of *Burramys* (picked out of some material before it was sieved) all cranial material in the reddish fraction comprised single bones dissociated from each other, whereas in the whitish fraction there were many cranial specimens comprising a number of individual bones firmly joined at the sutures.

2. Although both fractions of the deposit evidently originated as material regurgitated by owls in the form of pellets, no bones of the reddish fraction were found in pellets. By contrast, many partial and complete owl pellets were found containing bones of the whitish fraction.

3. Whereas the species represented in the whitish fraction comprised the local modern small mammal fauna, the reddish fraction contained some species not recorded, living or in any other fossil deposit, within several hundred miles of the Pyramids site. (See Table 1 and p. 8.)

4. Though the whole deposit had been accumulated in the one place, bones of the reddish fraction had undergone considerable change in

texture and colour while those of the whitish fraction had not.

Items 3 and 4 are further discussed on p. 9.

The sorting of the deposit into the two fractions was completed, and from each fraction bones were segregated as follows: (a) all cranial, dentary and dental material, (b) a selection of specimens of major post-cranial bones, and (c) a bulk of fragments for radiocarbon dating.

Cranial material and dentaries were identified at species level. As the dentary was almost invariably the most numerous recognizable bone of a species, dentaries were counted to provide data of species numbers in each fraction. Usually, to assess the minimum number for a species, right and left dentaries were counted separately and the greater figure accepted, but for very large groups a total dentary count was halved.

The number for each species and family in (a) the reddish fraction, and (b) the whitish fraction, are shown in Table 1, together with percentage which each species number represents of its fraction.

With the exception of the two wet forest species, *Schoinobates volans* and *Potorous tridactylus,* all small marsupials of which there are modern records from within 25 miles of the Pyramids are represented in the whitish fraction of the deposit. Of the two additional species in the fraction, *Gymnobelideus leadbeateri* was probably present during a phase of local conditions somewhat wetter than those of modern times, but *Petaurus norfolcensis* would have been present until the natural woodlands of *Eucalyptus melliodora* were cleared.

Of the murids, the two species of *Rattus* still occur within the 25-mile radius, and, before intensive grazing was established, the complex of woodland, stony hillslopes and wet grassy depressions of the limestone formation would have provided suitable habitat for *Conilurus, Pseudomys* spp. and *Mastacomys.* Before the decimation of this pseudomyine group, *Pseudomys fumeus* may have occurred in the ferny declivities of the Pyramids hill and along Shaws Creek and the river. *Hydromys* was evidently very rarely caught by the owls, and it is the only locally-recorded modern murid not found in the whitish fraction of the deposit.

Thus there is very close coincidence between the modern small mammal fauna of the region and the species of the whitish fraction. This is essentially a faunal assemblage of dry sclerophyll forest and grassy woodland (see pp. 2-6).

The composition of the reddish fraction of the deposit shows it to be, in general, a wet sclerophyll forest faunal assemblage, belonging to habitats

TABLE 1

Number and Percentage of Species in Pyramids Cave Deposit Fractions

	Reddish fraction		Whitish fraction	
	No.	%	No.	%
Sminthopsis leucopus	356	4.2	237	9.5
Antechinus stuartii	1,238	14.5	311	12.4
Antechinus swainsonii	390	4.6	98	3.9
Phascogale tapoatafa	19	0.2	2	0.1
Dasyurus viverrinus	1	0.0	2	0.1
Sarcophilus laniarius	1	0.0		
Dasyuridae	2,005	23.5	650	25.9
Perameles nasuta	81	0.9	26	1.0
Isoodon obesulus			20	0.8
Peramelidae	81	0.9	46	1.8
Acrobates pygmaeus	1,103	13.0	136	5.4
Cercartetus nanus	979	11.5	146	5.8
Cercartetus lepidus	111	1.3		
Burramys parvus	141	1.7		
Gymnobelideus leadbeateri	221	2.6	3	0.1
Petaurus breviceps	197	2.3	36	1.4
Petaurus norfolcensis			6	0.2
Petaurus australis			1	0.0
Pseudocheirus peregrinus	53	0.6	9	0.4
Schoinobates volans	5	0.1		
Trichosurus sp.			1	0.0
Phalangeridae	2,810	32.9	338	13.5
Potorous apicalis	14	0.2	13	0.5
Petrogale penicillata	1	0.0		
Macropodidae	15	0.2	13	0.5
Hydromys chrysogaster	1	0.0		
Rattus fuscipes assimilis	2,225	26.1	303	12.1
Rattus lutreolus	12	0.1	52	2.1
Pseudomys oralis			502	20.0
Pseudomys higginsi	165	1.9		
Pseudomys fumeus	817	9.6	225	9.0
Pseudomys novaehollandiae	43	0.5	134	5.3
Melomys cervinipes	38	0.4		
Mastacomys fuscus	97	1.1	194	7.7
Conilurus albipes	1	0.0	31	1.2
Muridae	3,399	39.9	1,441	57.5
Rhinolophus megaphyllus			1	0.0
Eptesicus pumilus	3	0.0	1	0.0
Chalinolobus morio	3	0.0		
Chalinolobus gouldii	3	0.0	1	0.0
Nyctophilus geoffroyi	29	0.3	8	0.3
Nyctophilus timoriensis	4	0.0	3	0.1
Pipistrellus tasmaniensis	6	0.1	3	0.1
Miniopterus schreibersii	153	1.8	1	0.0
Tadarida australis	1	0.0		
Tadarida loriae	2	0.0	1	0.0
Microchiroptera	204	2.4	19	0.8

considerably wetter than those of the modern fauna of the Pyramids area. The principal evidence is:

1. The predominance of *Rattus fuscipes assimilis* in the reddish fraction, where it comprises 26 per cent of the mammal count, compared with 12 per cent in the whitish fraction.

2. The strong representation of *Gymnobelideus* and *Burramys* in the reddish fraction and their low status or absence in the whitish fraction. Each requires very wet conditions, either forest or shrubbery.

3. The absence or low status in the reddish fraction of the woodland species *Petaurus norfolcensis* and *Conilurus albipes,* compared with the representation of each in the whitish fraction.

4. The low status of *Rattus lutreolus, Mastacomys fuscus* and *Pseudomys novaehollandiae* in the reddish fraction, compared with their strong representation in the whitish fraction. The first two favour wet grassed areas rather than dense forest, and the third is a dry forest species.

The following data, supplied by the FWD, are numbers of terrestrial mammals trapped at Loch Valley, east-central Victoria, during 1957-63. The general vegetational formation is wet sclerophyll forest and the M.A.R. is approximately 56 in.

Antechinus stuartii	83
Antechinus swainsonii	54
Perameles nasuta	13
Rattus fuscipes assimilis	1,408
Rattus lutreolus	3
Mastacomys fuscus	6

Gymnobelideus leadbeateri, Pseudocheirus peregrinus and *Schoinobates volans* were also recorded as present in the area.

Despite the different sampling method, the proportionate representation of the species in this list is very similar to that in the reddish fraction of the Pyramids deposit (Table 1).

Data in Table 1 demonstrate discontinuity in species composition between the two fractions of the deposit. *Cercartetus lepidus, Burramys parvus, Pseudomys higginsi* and *Melomys cervinipes* are not represented in the whitish fraction, while *Isoodon obesulus, Petaurus norfolcensis* and *Pseudomys oralis* are not in the reddish fraction. Furthermore, no bones intermediate in physical character between those of the two fractions were found in the deposit. These two features lead to the hypothesis that there was a time gap between the respective periods of accumulation of the two fractions.

Samples of typical hard bones of the whitish fraction, when baked for 30 days at 135°C, became fragile in texture and reddish-brown in colour, as in the reddish fraction. This applied equally to bones buried in a quantity of cave dust and to bones not in any matrix. Therefore, the fragile reddish state may be brought about by chemical alteration induced by heat and is not dependent on contact with the matrix.

In summary, the data indicate the following sequence in the Pyramids area:

1. An early phase when ground-moisture conditions were wetter than at present and the vegetational formation predominantly wet sclerophyll forest, and when the mammal fauna was similar to that of modern wet forests in high rainfall areas of east-central Victoria but with *Cercartetus lepidus, Melomys cervinipes* and *Pseudomys higginsi* also present.

2. An intermediate phase during which the predators did not use the Pyramids Cave and during which bones in the cave became altered to fragile texture and reddish colour.

3. A late phase when ground moisture and vegetational formations approximated those of the area at present, with a dry forest and woodland fauna essentially the same as the local modern one.

The comparative abundance of *Miniopterus schreibersii* in the reddish fraction would only indicate that this bat colonized the cave at some time during the early phase, and that natural mortality or owl predation added the remains of a number to the deposit.

COLOUR ANALYSIS OF REDDISH FRACTION

Between individual bones of the reddish fraction there was considerable variation in colour, from light orange to dark reddish-brown. With the idea that this variation might be correlated with age, dentaries of the fraction were sorted into six colour categories. For each category, a small group of specimens was selected as a standard. Sorting was done, by visual comparison, according to the standard to which each dentary approximated most closely. Only clean, uniformly coloured dentaries were included in this analysis, and the total sample sorted comprised approximately two-thirds of the dentaries of the reddish fraction. By the same process, post-cranial bones and bone fragments were sorted out from the reddish fraction, to provide samples of the colour categories for radiocarbon dating.

The categories are identified by the figures 5 to 10. According to the colour standards of Ridgway

TABLE 2

Number and Percentages of Principal Species and Families in Colour Categories of the Reddish Fraction, Pyramids Cave

Categories:	10		9		8		7		6		5	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Sminthopsis leucopus	62	5.4	67	4.8	48	4.0	21	2.3	17	3.7	0	0.0
Antechinus stuartii	166	14.4	181	13.1	196	16.2	109	12.1	52	11.4	16	10.4
Antechinus swainsonii	57	4.9	65	4.7	38	3.1	40	4.4	17	3.7	1	0.6
Phascogale tapoatafa	1	0.1	1	0.1	3	0.2	3	0.3	3	0.7	3	1.9
Dasyuridae	286	24.8	314	22.7	285	23.6	173	19.2	89	19.6	20	13.0
Perameles nasuta	5	0.4	6	0.4	12	1.0	9	1.0	8	1.8	3	1.9
Acrobates pygmaeus	206	17.9	178	12.9	115	9.5	53	5.9	17	3.7	4	2.6
Cercartetus nanus	104	9.0	129	9.3	135	11.2	158	17.7	79	17.4	35	22.7
Cercartetus lepidus	15	1.3	19	1.4	12	1.0	12	1.3	5	1.1	1	0.6
Burramys parvus	28	2.4	24	1.7	14	1.2	14	1.5	14	3.1	1	0.6
Gymnobelideus leadbeateri	30	2.6	30	2.2	26	2.1	25	2.8	18	4.0	0	0.0
Petaurus breviceps	27	2.3	35	2.5	29	2.4	24	2.7	9	2.0	3	1.9
Pseudocheirus peregrinus	4	0.3	9	0.7	7	0.6	7	0.8	6	1.3	3	1.9
Phalangeridae	414	35.9	425	30.8	338	27.9	293	32.6	150	33.0	49	31.8
Rattus fuscipes assimilis	336	29.2	462	33.4	373	30.8	247	27.5	102	22.4	25	16.2
Pseudomys higginsi	20	1.8	24	1.7	32	2.6	17	1.9	18	4.0	11	7.1
Pseudomys fumeus	76	6.6	122	8.8	146	12.1	128	14.2	70	15.4	35	22.7
Pseudomys novaehollandiae	4	0.3	11	0.8	4	0.3	4	0.4	1	0.2	1	0.6
Melomys cervinipes	4	0.3	7	0.5	4	0.3	2	0.2	1	0.2	0	0.0
Mastacomys fuscus	5	0.4	8	0.6	14	1.2	24	2.7	11	2.4	9	5.8
Muridae	445	38.6	636	46.0	573	47.4	423	47.1	205	45.1	81	52.6
Total, marsupials & murids	1,152		1,382		1,210		899		455		154	

Note: Numbers and percentages for families, and the final totals, include data of some species not listed in the table.

(1912), the sequence ranges from Pale Yellow-Orange (category 5), through Cinnamon Buff (7) and Cinnamon (8), to Sudan Brown (10). The number of individuals of each species represented in each category was estimated by counting the dentaries. Numbers for the principal species, and for the families, together with the percentage which these represent in each category, are set out in Table 2. Certain of these data are further illustrated in Fig. 2.

It was observed that reddish-brown bones of this fraction faded to appreciably lighter colours when kept for a period of approximately two years in open boxes subject to daylight and artificial light. Similar lots kept in closed boxes did not fade. This was assessed by comparison with standards used for the original sorting. The observation suggests that bones lying at and near the surface in the deposit would have attained lighter coloration. Furthermore, bones of category 5, as well as being of lightest colour, were in general the most fragile of the fraction, indicating greater exposure to the factors which induced change in texture.

The two observations suggest that, during the phase of alteration of the older fraction, bones became differentially coloured according to the various depths at which they lay. If the deposit remained essentially undisturbed until after the phase of alteration, variation in colour in the reddish fraction should be correlated with original stratification and hence with age. The fact that material of the whitish fraction was present throughout the deposit, particularly in the trough of the inner chamber, demonstrates that the movement of the bulk of the deposit from the outer
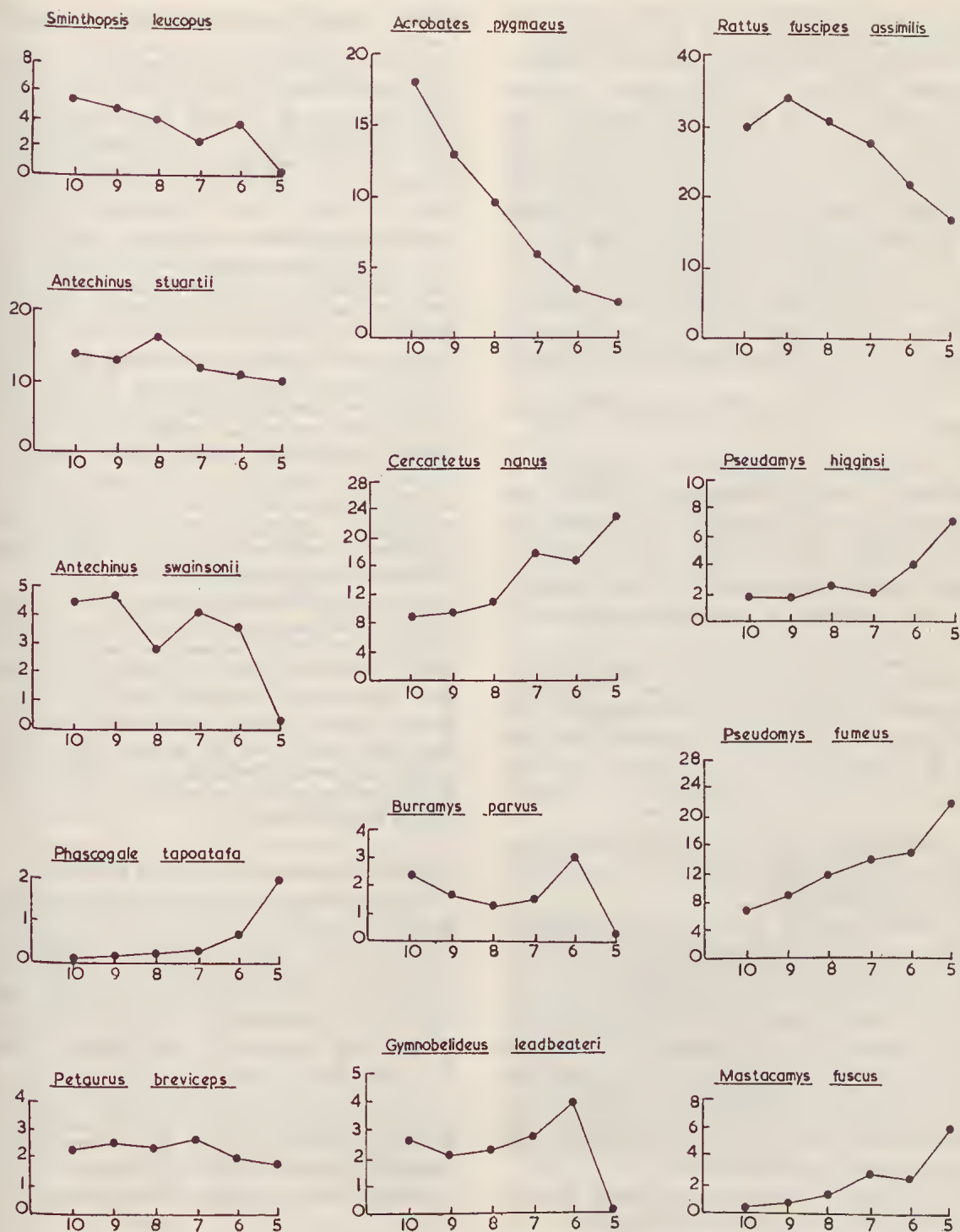
FIG. 2—Percentages of principal species in colour categories of reddish fraction of Pyramids Cave deposit. Percentages are shown on the vertical scale, and colour categories on the horizontal line, in each case.

chamber did in fact take place during or after the period of accumulation of the whitish fraction.

It would appear therefore that the six colour categories represent a chronological sequence, with category 10 the oldest and category 5 the youngest. The orderliness of results of the species analysis of the colour categories, as evidenced by steady trends in graphs of Fig. 2, support the colour-age correlation theory. The species analyses do not require absolute colour-age correlation for the individual specimens; they depend on the concept of mean age of the specimens of a species in a colour category, and such means should be independent of the amount or extent of overlap between a group of specimens and its counterparts in adjacent categories.

The following considerations arise from data in Table 2:

1. Through the sequence from category 10 to category 5, there is progressive decline in percentages of *Acrobates pygmaeus* and *Rattus fuscipes assimilis*, and there is progressive increase in percentages of *Phascogale tapoatafa, Cercartetus nanus* and *Mastacomys fuscus.* Statistically, this sequence of changing percentages is highly significant ($p < 0.001$).

As *Acrobates* and the *Rattus* are most abundant in dense wet forests, and the other three favour comparatively dry and/or open vegetational formations, these changes indicate that, over the period of accumulation of the reddish fraction, there was a general lessening of wet sclerophyll forest coverage in the Pyramids area.

2. Category 5 differs from the whitish fraction (Table 1) and other categories of the reddish fraction in these ways:

(a) Absence or very low status of *Sminthopsis leucopus, Antechinus swainsonii, Cercartetus lepidus, Burramys parvus, Gymnobelideus leadbeateri* and *Melomys cervinipes,* all of which favour comparatively wet habitats. In comparison with the overall proportions in categories 6 to 10 combined, the low proportions in category 5 are significant only for the less rare species; but when the data of the six species are combined to represent a unit of wet habitats, the same comparison gives a high level of significance ($p < 0.001$).

(b) The ratio of *Acrobates pygmaeus* to *Cercartetus nanus* is least (1:9) in category 5.

(c) The percentage of *Phascogale tapoatafa* is highest in category 5.

Category 5 thus appears to represent a faunal assemblage of habitats drier than those represented by the other reddish categories and drier than the average conditions during the accumulation of the whitish fraction of the deposit.

The last part of this comparison is reinforced by the close similarity in analysis between the owl pellet deposit from Victoria Range, western Victoria (Wakefield 1963b), and category 5, In both cases, murids comprise approximately half the mammal count, with *Pseudomys fumeus* the most abundant murid, while *Cercartetus nanus* contributes approximately 20 per cent of the mammal count and is the most abundant phalangerid. However, the higher percentage of *Antechinus swainsonii,* and the higher ratio of *Acrobates pygmaeus* to *Cercartetus nanus* (1:3), in the Victoria Range deposit, indicate that the latter accumulated in environmental conditions less dry than those applying to category 5. The Victoria Range area is today drier than the Pyramids area, and the fauna of the Victoria Range deposit, like that of the whitish fraction of the Pyramids deposit, is essentially the modern fauna of its area. By these comparisons, category 5 appears to represent environmental conditions much drier than modern conditions in the Pyramids area.

In summary, the colour analysis of the reddish fraction indicates (a) that during the period of accumulation of this fraction there was progressive change to less wet ground conditions and to more open vegetational formations, and (b) that the terminal stage of the accumulation represents conditions drier than the present and with the mammal fauna correspondingly modified by the elimination or marked reduction of species favouring wet forest habitats.

Colour Variation in Whitish Fraction

By a process similar to that used for the reddish fraction, dentaries of the whitish fraction were sorted into four colours: category 1, glossy white; category 2, dull white; category 3, yellowish white; category 4, greyish white. Clean post-cranial bones and bone fragments were sorted from the fraction to provide a sample each of categories 2 and 3 for radiocarbon dating.

Species counts were made, and the percentage of each species determined, for each category. No significant difference was found between the categories, either in species represented or in the proportionate representation of each species.

Age Estimates
Evidence from Other Deposits

The faunal, vegetational and climatic sequences indicated by the Pyramids Cave data conform very closely to those indicated by study of stratified sediments and fossils of McEacherns Cave,

Nelson, south-western Victoria (Wakefield 1967c, 1969a).

Nelson is 400 miles W. of the Pyramids, and altitude, geology, climate and general vegetation are about the same in both areas. McEacherns Cave was not a predator den but a trap into which ground-frequenting animals fell. There were three groups of sediments relevant to a comparison with the Pyramids deposit:

1. Lower sediments, containing remains of large extinct Pleistocene marsupials (*Zygomaturus, Protemnodon, Sthenurus* spp., *Thylacoleo* and *Sarcophilus laniarius*), and a small-mammal fauna of the wet sclerophyll forest type, with *Rattus fuscipes* comprising 44 per cent of the total mammal count, with *Antechinus stuartii* and *Perameles nasuta* next in abundance, with *Pseudomys fumeus* present but *Conilurus* and other pseudomyine murids absent, and with *Isoodon* absent. A radiocarbon date of 15,200 ± 320 years B.P., returned for a collection of small bones from the uppermost few inches of these sediments, identifies the sample with the latter part of the main Würm glacial period. (The age range represented in the sample may have been of the order of thousands of years, as the bones numbered several hundred and they and the associated sediments had probably been shifted to their final location by water movement.)

2. An intermediate group of sediments, comprising many thin strata of silt and fine sand, wind-eroded from various surface sediments and blown into the cave, overlain by coarse sand containing remains of semi-desert animals—*Onychogalea fraenata, Bettongia lesueur*, and a small form of *Isoodon*. The wind-blown sediments were superimposed on the lower (Pleistocene) sediments with marked disconformity between, indicating an abrupt reduction of underground water movement.

3. Upper sediments, containing the mammal species of the modern local dry sclerophyll forest and woodland fauna, including *Conilurus albipes*, four species of *Pseudomys*, and the large *Isoodon obesulus*, and with *Rattus fuscipes* represented by only 10 per cent of the total mammal count.

Fern Cave (16 miles E. of McEacherns Cave) contained a subfossil fauna essentially modern in character, with no semi-desert species or extinct Pleistocene marsupials, but *Thylacinus* was represented. This fauna is very similar, both in species composition and proportionate representation, to that of the upper sediments in McEacherns Cave (Wakefield 1964, 1967c). On the basis of the most recent dates for *Thylacinus* remains on the Australian mainland (Macintosh and Mahoney 1964, Partridge 1967, Lowry and Merrilees 1969),

the probable period of accumulation of the Fern Cave deposit may be assessed as extending from the order of 3,000 to 4,000 years B.P. to the present.

The main part of the reddish fraction of the Pyramids deposit appears to correspond to the lower (Pleistocene) sediments and fossils of McEacherns Cave. Category 5 of the reddish fraction, and the hiatus between the periods of accumulation of the two fractions of the Pyramids deposit, appear, collectively, to correspond to the phase of wind-blown dust in McEacherns Cave and to the occurrence of semi-desert fauna there. The whitish fraction of the Pyramids deposit corresponds to the faunal assemblage of the upper sediments of McEacherns Cave and to the whole of the Fern Cave deposit.

Of the semi-desert mammals appearing in McEacherns Cave, *Bettongia lesueur* may be used as an indicator of climatic conditions. It is not recorded as a modern animal in Victoria but occurred in the Murray-Darling Junction area, south-western New South Wales, in 1857, where M.A.R. is 10 in. (Wakefield 1966). Its extension south to coastal areas of western Victoria, where M.A.R. exceeds 25 in., would point to conditions drier than the present. The suggestion is strengthened by the association of the species with the wind-blown sediments in McEacherns Cave. Moreover, the absence of the species from comparatively recent south-western Victorian subfossil sites, such as Fern Cave, indicates that in this region it belonged to conditions different from those of modern time.

Bettongia lesueur has been found also, in southwestern Victoria, in deposits at Skene Street, Warrnambool, and at Mount Hamilton. In both cases the range of mammals embraced extinct Pleistocene species, such as *Sthenurus* and *Thylacoleo*, and modern introduced species such as *Ovis* and *Mus*. Neither the *Bettongia* nor any extinct Pleistocene species occurred in the Tower Hill beach middens, 7 miles WNW. of Warrnambool, where the assemblage is essentially the local modern one. (Wakefield 1964.) The main Tower Hill beach midden deposit lay in the lower horizon which provided a radiocarbon date, from charcoal, of 5,120 ± 120 years B.P. (Gill 1971).

Bettongia lesueur occurred, as the most abundant macropodid, in an aboriginal midden underlying the tuff from the Tower Hill volcano, at Merri Creek, Bushfield, 5 miles N. of Warrnambool, and was associated there only with species which persisted in the region into modern time (Wakefield 1964). At present, the most reliable evidence of the timing of the initial deposition of tuff in that area is a radiocarbon date of 7,300 ±

150 years B.P. (GaK-2856) obtained from solid pieces of marine shell from an aboriginal midden in tuff at Point Pickering, Warrnambool. Apparently this site was used during the period when Tower Hill was erupting. This date is more relevant than the 6,605 ± 90 years B.P. previously obtained for carbonate from bones in the Bushfield midden (Gill 1971), as the latter probably dates soil carbonate which the bones had acquired rather than the bones themselves. (The date for the Point Pickering midden, and associated comments, were made available by E. D. Gill in a personal communication.) These details indicate that *Bettongia lesueur* occurred at Bushfield dura period prior to 7,300 years B.P.

The Wombeyan Caves fauna included extinct Pleistocene marsupials, and also small mammals such as *Burramys parvus, Cercartetus lepidus* and *Pseudomys higginsi*, and it was evidently contemporaneous with the fauna of the reddish fraction of the Pyramids Cave deposit (see pp. 22, 24).

The owl pellet accumulation at Mabel Cave, East Buchan (4 miles SSE. of the Pyramids site), which was very similar to the whitish fraction of the Pyramids deposit, both in species present and their proportionate representation (Wakefield 1960a, 1960b), was later found to comprise the uppermost layer of a stratified deposit (Wakefield 1967b). The stratigraphic position of the Mabel Cave pellet material—from surface to several inches deep—and its similarity to the whitish Pyramids fraction, add to evidence that the latter was comparatively recent in origin.

RADIOCARBON DATING

Seven samples were extracted from the Pyramids Cave deposit for dating at Gakushuin University, Tokyo. Comparatively large clean bones and bone fragments were selected from material remaining after dentaries, cranial specimens and limb-bones were segregated, and these were sorted into the various colour categories. The selection was made from throughout the complete bulk of the bone debris from the deposit, so that each sample represented the whole of its colour category.

Advice had been received from Gakushuin University that samples weighing more than 150 gm. could be assayed (K. Kigoshi, letter 27 July 1965). The process of selection was continued until samples weighing between 200 and 240 gm. were obtained. To provide sufficient weight, material representing categories 5 and 6 was bulked to constitute sample 5–6. Other samples were numbered according to the category represented. The samples were sent in three stages—first nos. 3,

5-6, 8, 10; then 2, 9; then 7. Age assays for the samples were (years B.P.):

2.	(=GaK-1103)—	$\begin{cases} 2,530 \pm 90 \\ 3,260 \pm 400 \end{cases}$
3.	(=GaK-877)	—>33,000
5–6.	(=GaK-865) —	29,400 ± 1500
7.	(=GaK-1419)—	30,300 $\begin{cases} +2,400 \\ -1,700 \end{cases}$
8.	(=GaK-864) —	15,450 ± 600
9.	(=GaK-1104)—	17,700 ± 900
10.	(=GaK-863)	—>32,900

The younger date was reported initially for sample 2 (K. Kigoshi, letter 10 April 1967), and later (letter 17 April 1968) the older date was reported, with the explanation that the 2,530 was from carbon obtained by 'the usual H_2SO_4 extraction' while the 3,260 was obtained by 'the collagen method'. Earlier correspondence (4 July 1966) indicated that assays of bone samples were based on organic carbon.

The ages reported for sample 3 and sample 2 are incompatible. The two samples differed only in that the fragments comprising the one averaged somewhat yellowish in comparison with the average colour in the other. Each sample was extracted from throughout the whole of the whitish fraction of the deposit, there was no clear-cut differentiation in colour between the two, and all degrees of intermediate coloration were represented in the fragments allocated to the two samples. The colour categories which the samples represent are the same in faunal composition (see p. 12), the equivalent of the modern local mammal assemblage.

There is an anomaly also in the series of dates returned for samples from the reddish fraction. Again, the fragments making up each sample were obtained from throughout the whole of the bone debris of the fraction, the categories which the samples represent are not clear cut and each differs only slightly in average colour from the next. If difference in colour is, in fact, correlated with age, the series of samples (5–6, 7, 8, 9, 10) should have provided, in that order, either progressively greater or progressively smaller ages. If colour and age are not correlated, the samples, in view of the selection technique, should have given assays of the same order of age. It does not appear possible that true ages of the two samples of lightest colour (5–6 and 7) *and* the sample of darkest colour (10) were each about 30,000 years or more while the true ages of samples of intermediate colour (8 and 9) were each only about half as much.

Professor Kigoshi stated (letter 18 July 1966) that the following amounts of organic carbon were recovered from the first group of samples:

3. (GaK-877)—2·45 gm.
5–6. (GaK-865)—1·39 gm.
8. (GaK-864)—1·23 gm.
10. (GaK-863)—1·87 gm.

It was expected that, for those samples of similar qualities and comparable weights, less organic carbon would be recovered from older samples. However, for these four, the amounts were directly proportional to ages reported.

Corresponding data for later samples (letter 5 March 1968) are:

7. (GaK-1417)—1·10 gm.
9. (GaK-1104)—0·62 gm.

(The figure for sample 2 was not given.)

The carbon recovered for sample 9 (dated 17,700 years) was only one-third as much as for sample 10 (dated 32,000 years).

Additional samples are being extracted from the two fractions of the deposit, to be dated by the technique described by Haynes (1968). In the meantime, none of the radiocarbon dates already obtained for samples from the Pyramids Cave are advanced as evidence of ages of local events.

CLIMATOLOGICAL DATA

Further to the palaeoclimatic data discussed in the McEacherns Cave reports and the estimates made there (Wakefield 1967c, 1969a), the following details are relevant to assessment of dates for events in that locality and in the Pyramids area.

1. Rosholt *et al.* (1961) produced a 'generalized temperature curve' for surface waters of tropical seas, which showed (a) a period of very low temperature from 20,000 to 12,000 years B.P., corresponding to the main phase of the Würm glaciation, (b) rapid rise in temperatures from 12,000 to 10,000 years, with a thermal peak (a little below present level) 10,000 years ago, (c) a minor cold oscillation between 10,000 and 7,000 years ago, with its minimum at about 8,500 years, and (d) a period, from 7,000 years to the present, of temperatures higher than the present, with a thermal maximum about 4,000 years ago.

2. In a summary of climatic events, Dury (1967) included reference to (a) mean temperature rises of 17°C in Denmark, (b) 8°C or more in Columbia, and (c) from 'arctic to warm-temperate' in Austria, over the period 20,000 to 5,000 or 6,000 years B.P.; and he states: 'It seems impossible to escape the conviction that Australia has experienced major shifts in low-level air temperatures, synchronous with, similar in value to, and identical in direction with those which are abundantly demonstrated for other areas of the world.'

3. Crocker and Wood (1947) postulated a 'great Australian arid period', which they suggested had occurred 'about 4,000 to 6,000 years ago'. They gave evidence of 'widespread wind erosion . . . following the wholesale destruction of the local flora', and considered that 'the aridity must have been not only extremely severe, but its onset must have been particularly sudden'. The authors included the Nelson area in their region of wind erosion.

4. After considering available data from Australian Quaternary fossil deposits, Tedford (1967) concluded that 'as nearly as can be determined, the extinction of such genera as *Diprotodon*, *Sthenurus*, *Procoptodon* and *Protemnodon* took place at the very end of the last glacial period, a time surprisingly close to the average date of extinction for the larger placental herbivores of North America'.

5. Lundelius (1967) summarizes data of the late-Pleistocene and post-Pleistocene faunal sequence of central Texas. The post-Wisconsin (Würm) faunal history there involves (a) extinction of giant Pleistocene species, (b) northward withdrawal, or shrinkage to local relicts, of certain species dependent on wetter and cooler climates, and (c) augmentation of the remaining recent fauna by arrival of new forms. This is interpreted as showing a gradual drying of the climate, and an 'increase in seasonality' resulting in destruction of essential habitats by summer extremes. Pleistocene extinction in central Texas appears to coincide with that of other areas of North America, and the Texas data indicate that the widespread extinction coincided with the beginning of the climatic change at the end of the Pleistocene. In central Texas, all the dated fossil deposits containing extinct species are older than 10,000 years, and all faunas younger than 7,800 years contain only Recent (Holocene) species. (None of the Texan faunas belong to the critical period between these two dates.) There is no evidence from the Texas faunas that the climate of 4,000 to 6,000 years ago was drier or warmer than at present but there is evidence of wetter conditions about 5,000 years ago, which supports others' conclusions that in south-western North America the Altithermal was comparatively wet.

6. Studies of eucalypt pollen by Churchill (1968) demonstrate that in south-western Aus-

tralia the climate from at least 6,000 years B.P. until 4,000 B.P. was wetter than at present.

The characteristics of the reddish fraction of the Pyramids deposit (see p. 12) are what would be expected in a deposit accumulated during the general phase of rising world temperatures noted by Rosholt *et al.* and Dury. The extent of change in faunal composition in the fraction, indicated by the colour analysis, suggests a period of accumulation including all or most of the recession phase following the peak, about 20,000 years ago, of the main Würm glaciation.

The aeolian sediments found in McEacherns Cave require that there was a phase of wind erosion of surface sediments as postulated by Crocker and Wood, and the abrupt disconformity between those sediments and the essentially uniform underlying Pleistocene stratum in the cave

strongly support the contention of sudden aridity. The abrupt collapse of the wet forest fauna of the Pyramids area, evidenced by the nature of category 5 of the deposit there, would be consistent with a sudden onset of aridity. The McEacherns Cave sediments indicate that there was only a single phase of severe aridity, and the evidence of wet climate in south-western Australia 4,000 to 6,000 years ago, and of *Bettongia lesueur* at Bushfield more than 7,300 years ago, indicates that this phase was much earlier than the time suggested by Crocker and Wood.

The faunal and climatic sequences which Lundelius outlines for central Texas are so similar in detail to those which local cave deposits indicate for south-eastern Australia that the coincidence must be considered. The close analogy strengthens Tedford's suggestion that extinctions of large mar-

TABLE 3

Proposed Correlation of Pyramids Cave Data

Events at Pyramids Cave	Mammals of Pyramids area	Vegetation (Pyramids)	Climate (SE. Aust.)	Contemporaneous events	Epoch
Owls again occupy cave, accumulation of new pellet material in outer chamber, no alteration of bones, mixing together of old and new material by gravitational movement from outer to inner chamber probably assisted by possums.	Small mammal fauna similar to modern dry forest and woodland assemblage, presence of some species (Petaurus norfolcensis, Isoodon obesulus, Pseudomys oralis) not previously in evidence.	Mainly woodland and dry sclerophyll forest, as at present.	Average conditions similar to those of modern times.	Accumulation of upper sediments in McEacherns Cave, of complete Fern Cave deposit, and of owl-pellet layer in Mabel Cave, each with fauna equivalent to modern local assemblage.	H O L O C E N E
Owls absent, bones in existing deposit altered to fragile texture and reddish colour, those near surface attaining greater fragility and paler colour.	Not known.	Not known.	Drier than at present.	Presence of semi-desert mammals in SW. Vict., age assessment of > 7,300 B.P. for bones at Bushfield.	
	Disappearance of species dependent on wet forest habitats.	Destruction of forest habitats.	Abrupt change to aridity.	McEacherns Cave deposition changes abruptly to wind-borne dust.	
Following lowering of talus, occupation of cave by owls, accumulation of stratified deposit of pellet material in outer chamber, little or no movement of bones to inner chamber.	Essentially wet forest fauna but progressively changing to assemblage of less wet habitats; Sarcophilus laniarius, Cercartetus lepidus, Pseudomys higginsi and Melomys cervinipes present.	Formation mainly wet sclerophyll forest but long-term change to more open, less wet vegetation.	Colder than at present but with progressive change to less cold conditions.	Accumulation of lower sediments in McEacherns Cave, with wet forest fauna and extinct giant species, age ∿ 15,200 B.P. for associated bones; Wombeyan faunas include Cercartetus lepidus, Pseudomys higginsi and extinct giant species.	P L E I S T O C E N E
Talus reaches close to outer chamber.					

supials in Australia and of large placentals in North America were contemporaneous. If these events were indeed associated with a global pattern of climatic change, similar effects might be expected at comparable latitudes in the two continents.

CONCLUSION

The available evidence leads to the proposed correlation, set out in Table 3, between Pyramids Cave data and other events. There appears to be general harmony in this synthesis, and it is presented as the simplest interpretation of the data.

The small mammal assemblage represented in the reddish fraction of the Pyramids deposit is identified as Pleistocene. It was evidently a component of a fauna which embraced large marsupials such as *Zygomaturus*, *Sthenurus* and *Thylacoleo*. The fraction was probably accumulated, mainly or wholly, during the recession from the peak of the main Würm glaciation, from approximately 20,000 to the order of 10,000 years ago.

Extinction of the large marsupials, and fragmentation of the small assemblage (including disappearance of *Cercartetus lepidus* and *Pseudomys higginsi* from the Australian mainland and withdrawal northwards of *Melomys cervinipes*), appear to be related phenomena, associated with an early Holocene phase of aridity. These events may have been contemporaneous with similar events in North America approximately 8,000 to 10,000 years ago.

The assemblage of small mammals represented in the whitish fraction of the Pyramids deposit is identified as Holocene. It is evidently a component of a fauna comprising local species which survived the collapse of the Pleistocene fauna, and others (such as *Isoodon obesulus* and *Pseudomys oralis*) which moved in from elsewhere. The actual period of accumulation of the whitish fraction of the deposit is not assessed, but it is likely to have been several thousand years.

PLEISTOCENE AND HOLOCENE SERIES

From the material of each species represented in each fraction of the deposit, a series of cranial specimens and dentaries was selected for measurement and comparison of population parameters. Series are referred to as Pleistocene or Holocene, according to fraction. With minor exceptions the selection was limited to right dentaries and specimens which included the right maxilla. Series of modern museum specimens were included in the study. Unless otherwise indicated, modern series are Victorian, and the registered numbers cited in this section are those of the NMV.

Measurements were made with dial calipers or vernier calipers, correct to one-tenth millimetre. Unless otherwise indicated, measurements given are in millimetres. In general, quantitative comparisons in this section apply to means for the series concerned. Differences were assessed by the Student's t test, and those commented upon without qualification in this section are of high statistical significance, with $p < 0.01$.

The details set out are salient points extracted from a large volume of unpublished statistical data (Wakefield 1969b). For most species, especially where large numbers of specimens were involved, some significant differences were observed between the various series compared. Most of the differences however are of the order of those expected between local populations of a subspecies, and are less than those which usually distinguish primary subdivisions (=subspecies) of a species.

Ride (1960) noted that most specimens from Wombeyan Caves were subadult. This applies to owl pellet deposits in general, but it concerns marsupial specimens rather than murids. As a result, for many marsupial species, mean dimensions of bones subject to growth during subadult to adult stages were smaller in most Pyramids series than in modern museum series. In these cases, proportions of cranial bones and dimensions of teeth have been the main criteria for the comparisons.

DASYURIDAE

Sminthopsis leucopus

Teeth of the Pleistocene series are similar in size to those of a modern series from central and western Victoria, but lengths of molar rows of the Holocene series are 6 per cent less, suggesting an east-west dichotomy in the more recent Victorian populations.

Antechinus stuartii

Molar rows in the Pleistocene series are 2-3 per cent longer than in the Holcene series, but the M^{1-3} lengths of both series fit into the north-south size cline found in the species by Wakefield and Warncke (1967).

Antechinus swainsonii

The two Pyramids series are closely similar, but each has larger dentaries, larger molars and a more abruptly elevated coronoid process than in a modern series from Loch Valley, east-central Victoria. Wakefield and Warneke (1963) found that populations of the species from various south-eastern Australian localities differed without apparent pattern in features such as tooth-size.

PERAMELIDAE

Perameles nasuta

In the Pleistocene series, dentaries and premolar rows are 20 per cent shorter, and molar rows 11 per cent shorter, than in a modern series. No specimens with

mature dentition occurred in the Holocene fraction, but specimens from Basin Creek (in NMV) demonstrate that modern *P. nasuta* of the Pyramids area is large, as in other parts of Victoria. The smaller dimensions in the Pleistocene series may be due partly or wholly to an age bias between samples.

PHALANGERIDAE
Cercartetus nanus

The small modern series available is bimodal, with teeth dimensions in four specimens from eastern Victoria and eastern N.S.W. averaging 9 per cent more than in eight specimens from elsewhere in Victoria. The Holocene series corresponds in tooth-size to the four eastern specimens, but teeth dimensions in the Pleistocene series are 5 per cent more.

Burramys parvus

The modern Mt. Hotham specimen (C7290) is larger in limbs and molar teeth but smaller in premolars and it has a proportionately longer and narrower palate than the Pleistocene Pyramids *Burramys*. Differences are of various levels of significance.

Gymnobelideus leadbeateri

Teeth measurements of the Pleistocene series are 0-9 per cent more than in a modern series, with various levels of significance.

Petaurus breviceps

In the Pleistocene series, molars are not significantly larger, but fourth premolars are 7 per cent longer and wider than in the Holocene series, and the limb-bones are shorter by 7-10 per cent than in the Holocene and modern series. The apparent evolutionary elongation of limb-bones is being studied further.

Schoinobates volans

The Pleistocene series (dentaries only) has the molar row 7 per cent shorter than in a modern series. Seven Basin Creek specimens (in NMV) demonstrate that modern Pyramids district specimens have the larger molar size. The Pleistocene *Schoinobates* approaches in tooth-size the *S. volans minor* of north-eastern Queensland, a specimen of which, according to Thomas (1888) has molar teeth 10 per cent smaller than in the nominate race.

Pseudocheirus peregrinus

Teeth measurements in the Holocene series are 5-10 per cent more than in a modern series from central and south-eastern Victoria, indicating geographical variation in the recent population. The Pleistocene series has molars intermediate in size, but the P_4 smaller, than in either of the later series.

MACROPODIDAE
Potorous apicalis

The diagnostic P^4 of *P. apicalis* occurs on one Holocene Pyramids specimen, and there are specifically identified specimens also from other recent deposits in the area. However, as there is no P^4 available in the older fraction, the identification of the Pleistocene

Pyramids series as *P. apicalis* rather than *P. tridactylus* is tentative. Teeth of the Pleistocene series are, on the average, smaller than those of the Holocene and of modern series of *P. apicalis*.

MURIDAE
Hydromys chrysogaster

Size of the single M^1 (Pleistocene) approximates to the minimum observed in a modern series.

Rattus fuscipes assimilis

The zygomatic plate is proportionately longer in the Pleistocene series than in the Holocene and a modern series.

Pseudomys fumeus

The Pleistocene and Holocene series are generally similar, but they differ, collectively, from the topotypical modern western Victorian series by smaller sizes of teeth and cranial bones.

Pseudomys higginsi

This presumably extinct mainland population is discussed elsewhere (Wakefield 1972). Its teeth are larger and the zygomatic plate proportionately longer than in the modern Tasmanian population.

Pseudomys oralis

In the holotype (BM, 47.1.20.2), M^{1-3} length (alveolar) is $6 \cdot 8$, and the interorbital constriction is $3 \cdot 7$ (J. E. Hill, letter 12 March 1965). M^{1-3} length in the Holocene series is similar (mean $6 \cdot 9$) but the interorbital constriction broader (n, 15; mean, $4 \cdot 26$; s.d., $0 \cdot 18$).

Pseudomys novaehollandiae

The Pleistocene and Holocene series are similar in teeth measurements, and these are 5 per cent more than in a topotypical series from north-eastern New South Wales, according to measurements of Keith and Calaby (1968).

Conilurus albipes

Specimens of the Holocene series, submitted to the BM, 'suggest a larger, wider skull with longer tooth-rows' than available comparative material 'including BM 42.6.29.8, described by Tate (The Rodents of Australia and New Guinea, *Bull. Amer. Mus. Nat. Hist.* 1951, 97: 183-430, p. 270) in which M^{1-3} (crowns) is $8 \cdot 5$ mm and not $9 \cdot 5$ as he states (pp. 270, 370)' (J. E. Hill, letter 13 July 1967).

Mastacomys fuseus

In the Pleistocene series teeth are smaller and the zygomatic plate proportionately longer than in the Holocene series, while the latter is generally similar to a modern series from the Australian mainland. The populations of the species are reviewed elsewhere (Wakefield 1972).

Other species in the Pyramids deposit showed little variation between series from the two fractions or between these and modern museum series.

WOMBEYAN CAVES

MAMMALS OF THE FOSSIL BRECCIA

Broom (1896a, 1896b, 1896e) described specimens of marsupials from a deposit of bone breccia at Wombeyan Caves, eastern New South Wales, and Ride (1956a, 1956b, 1960) made further study of material from the same source. Some of Broom's specimens (in AM), and certain additional ones studied by Ride, have been examined, and in this section a summary is presented of the species and their principal characters. In most cases the characters are assessed on the basis of data from pp. 17-18, and the same system of annotation is used, except that the unqualified specimen numbers hereunder are those of the AM.

Besides adjustments arising from synonymies discussed later (pp. 20-22), three alterations are made here to identifications of Ride (1960). A specimen (B61) included then in the *Antechinus flavipes* series is identified as *Sminthopsis murina*, one (B8/g) included then in the *Pseudomys oralis* series is identified as *Pseudomys higginsi*, and the series then named *Gyomys glaucus* is identified as *Pseudomys fumeus*. Schram and Turnbull (1970) also used the name *Gyomys glaucus* for a series of *Pseudomys fumeus* from the Wombeyan Caves breccia.

Sminthopsis murina

Ride's B61, a dentary, has tooth-sizes and comparatively short premolar row as in a modern southeastern Australian series of *S. murina*. In *S. leucopus* the premolar row is relatively long.

Antechinus flavipes

The typical molar row lengths and the diagnostic proportionate lengths of premolar rows confirm the identity of Ride's B59 (maxilla) and B18 (dentary).

(Phascogale tapoatafa)

The specimens reported by Ride (1960) were not examined.

Isoodon macrourus (syn. Perameles wombeyensis Broom)

Comparatively large tooth-sizes and the montane habitat identify F4198 and Ride's B24 as *I. macrourus* rather than *I. obesulus,* but the diagnostic M^4 is not available in the Wombeyan specimens to confirm the identification. (See p. 20, under *Perameles wombeyensis.*)

Perameles nasuta

The angle at which the anterior edge of the coronoid process ascends from the line of the ramus and the curvature of the lower edge of the posterior part of the ramus, in F51878, and the form of the three premolars in F51879, identify the two specimens as *P. nasuta.*

Cercartetus nanus

F17502, Ride's B17/i, B17/ii (maxillae), B16 and B56 (dentaries), have the large tooth-size of the Pleistocene Pyramids series.

Cercartetus lepidus

The few available measurements of Ride's B8 are closely similar to those in the Pleistocene Pyramids series.

Burramys parvus

Five specimens—F3984 (type), F45778 (dentaries), F45777 and Ride's B59 and B8a (maxillae)—have teeth smaller than those of the Pleistocene Pyramids series, but proportions are closely similar. However, measurements noted by Ride (1957a) for a specimen (B57) not available during the present study, indicate a proportionately very long diastema.

Gymnobelideus leadbeateri (syn. Palaeopetaurus elegans Broom)

F17501 and Ride's B46 (dentaries) are not separable from a modern Victorian series (topotypical). See pp. 20-21, under *Palaeopetaurus elegans.*)

Petaurus breviceps

Ride's B18 (maxilla) has tooth-sizes smaller than means found in Pyramids and modern Victorian series.

Schoinobates volans

The identification of F5188 (dentary) is discussed under *Pseudocheirus antiquus* on page 21.

Pseudocheirus peregrinus (syn. Pseudocheirus antiquus Broom)

P4196 and Ride's B16 (maxillae) have tooth-lengths 12-15 per cent more than in the modern central and south-eastern Victorian series, and the intermediate sizes in the Pyramids series suggest a clinal gradient in this feature. (See p. 21, under *Pseudocheirus antiquus.*)

Potorous tridactylus

F4201 and Ride's B17 (maxillae), and F51880 (dentary), have tooth-sizes less than in a modern south-eastern Australian series of *P. tridactylus.* (See p. 21.)

Wallabia bicolor (syn. Macropus wombeyensis Broom)

F4199 (dentary) is typical of the eastern Australian population. (See p. 21, under *M. wombeyensis*).

Rattus fuscipes

Three molar teeth have been examined from the specimens identified by Schram and Turnbull (1970) as *Rattus* sp. These are comparable in dimensions with those of *R. fuscipes.* Four maxillae from the recently discovered Wombeyan Caves quarry deposit (Hope 1971) are identified, on the evidence of posterior shape of incisive foramina, as *R. fuscipes.*

Pseudomys oralis

Except for narrower incisive foramina, dimensions and proportions in Ride's B58/b (incomplete skull) and B58/c (dentary) correspond closely to data of the Holocene Pyramids series.

Pseudomys higginsi

Three measurements and one ratio, available in Ride's B8/g (dentary), are almost coincident with means in the Pleistocene Pyramids series. Four maxillae from the Wombeyan Caves quarry deposit confirm that there was a population in that locality of the Pyramids form of *P. higginsi* (Wakefield 1972).

Pseudomys fumeus

Ride's D8/6, D20/zii (maxillae), D20L, B59/i and B59/ii (dentaries), have teeth dimensions approximately 10 per cent less than in modern topotypical western Victorian series but similar to those of the two Pyramids series.

Mastacomys fuscus (syn. M. wombeyensis Ride)

See also pp. 21-22. Specimens from the Wombeyan Caves quarry deposit have similar characters (comparatively small teeth and proportionately long zygomatic plate) to those of the Pleistocene Pyramids series (Wakefield 1972).

TAXONOMY OF WOMBEYAN NOVELTIES

Perameles wombeyensis Broom

In the original diagnosis Broom (1896e) used several specimens (syntypes), which he figured in Plate VIII of his paper.

The Figs. 1 and 8 of that plate are of F4198 (AM), an incomplete dentary with the M_2 present. The abruptly elevated coronoid process identifies the specimen as *Isoodon* and not *Perameles*, and the size of the molar (length 2·8 mm) is that of *I. macrourus*. *I. macrourus* is widely distributed in the Blue Mountains, while the smaller *I. obesulus* is typically lowland and near-coastal.

Broom's Fig. 2 is of a specimen with upper premolars and canine, which teeth Broom described. This specimen was not available for the present study but it appears to be of *I. macrourus*.

Broom's Figs. 3 and 4 are of F51879 and F51878 respectively, which are incomplete dentaries of *Perameles nasuta* (see p. 19, and Pl. 3, fig. 2, 4, this paper).

Broom's Figs. 5, 6 and 7, are single teeth, apparently of *P. nasuta*.

Broom described *P. wombeyensis* as 'a little larger than *P. obesula*' (i.e. *Isoodon obesulus*), and in particular the upper canine and the P^1 (length 2·8 mm) were said to be longer than those of *obesulus*. These data, and features of the coronoid process, were obtained from the specimen of his Fig. 2 and F4198. Broom did not compare *wombeyensis* with *macrourus* (or its synonym, *torosus*).

F4198 (Pl. 3, fig. 1, this paper) is here nominated LECTOTYPE of *Perameles wombeyensis* Broom. The specimen of Broom's Fig. 2 remains as a PARATYPE; and F51878 and F51879, as well as the specimens of Figs. 5, 6 and 7, are excluded from the diagnosis.

Perameles wombeyensis should be placed in the synonymy of *Isoodon macrourus*.

Palaeopetaurus elegans

Broom (1896b) described *Palaeopetaurus elegans* from five specimens, three of which he figures in Plate XLVI of his paper, as follows: Fig. 1. Cranial fragments and teeth, pieced together. Fig. 2. An incomplete dentary. Fig. 3. Dentary fragment with M_1 and M_2.

Of the syntype specimens, that of Fig. 2 of the plate is F17501 (AM), and that of Fig. 3 is Ride's B46, noted earlier (p. 19) as *Gymnobelideus leadbeateri*. The location of the specimen(s) comprising Broom's Fig. 1 is unknown.

F17501 is not distinguishable in any observed detail from *Gymnobelideus leadbeateri*, having the same almost straight incisor, low coronoid process, and slightly deflected angle, which distinguish this species from *Petaurus breviceps*. The shape of the masseteric fossa of the specimen is also as in *Gymnobelideus*. McCoy (1867) did not illustrate this feature accurately in the original diagnosis of *G. leadbeateri*, which misled Broom, who noted the difference between his specimen and McCoy's illustration.

Broom noted that in *Palaeopetaurus elegans* the 'frontal bones . . . present a remarkable resemblance to those of *Gymnobelideus*, and differ from those of *Petaurus* in the absence of the post-orbital ridge'.

He described characters of the upper teeth from the specimen illustrated in his Fig. 1. The P^1 is described as 'single-rooted', but this is modified later (Broom 1896e) to 'its two roots were united together'. The P^3 of the original diagnosis had a 'very low crown as in *Petaurus*' and 'two well developed divergent roots'. The M^1 is described as 'having the two inner cusps very small and brought together', and the M^2 as 'apparently similar to' the M^1. Later, Broom (1896e) referred to 'two other specimens of *Palaeopetaurus elegans*' in which the P^1 of the one had 'the roots close together but distinct', while the P^1 of the other had 'the roots somewhat apart'.

Broom (1896e) recorded two specimens of *Petaurus breviceps* from the Wombeyan breccia: 'an imperfect fragment of a lower jaw', and 'a fragment of the cranium with the frontal bones almost perfect', but he did not record any maxilla or upper teeth. The evidence indicates that the three maxillary specimens which he attributed to *Palaeopetaurus elegans*, including the syntype of his Fig. 1, are in fact *Petaurus breviceps*. (In *P. breviceps* both P^1 and P^3 are 2-rooted, while in

Gymnobelideus each is single-rooted.) However, there remain some anomalies in that Broom's description of the M^1 fits the M^1 of *Gymnobelideus* rather than that of *Petaurus breviceps*, while the 'apparently similar' M^2 would fit neither *Petaurus* nor *Gymnobelideus*, each of which has that tooth more square in cross-section.

F17501 (Pl. 3, fig. 3, this paper) is here nominated LECTOTYPE of *Palaeopetaurus elegans*. Ride's B46 remains as a PARATYPE, and the specimen(s) comprising Broom's Fig. 1, and its features, are excluded from the diagnosis.

Palaeopetaurus elegans should be placed in the synonymy of *Gymnobelideus leadbeateri*.

Pseudocheirus antiquus Broom

Broom (1896c) based this on several specimens, including F4196 and F51881 (AM), which he illustrated in Fig. 4, and in Figs. 6 and 8, of Plate VII of his paper. (F51881 now lacks the molar which Broom illustrated with it.)

The proportion P^3 width/P^4 width ($=0\cdot71$) in F4196 identifies this specimen as *Pseudocheirus peregrinus* rather than *Schoinobates volans*. In modern Victorian series of these species, means of this proportion were equivalent to $0\cdot80$ and $0\cdot90$ respectively.

The 'angle of jaw relatively small and passing backwards but a short distance' of Broom's diagnosis applies to specimen F51881, and this is, in fact, a diagnostic character of *Schoinobates volans* (Wakefield 1960a). (See Pl. 3, fig. 8, this paper.)

Other characters by which Broom sought to distinguish the *P. antiquus* from *P. peregrinus* appear to reflect characters of individuals used in the comparisons rather than true differences between populations, and a number of the characters which he found in the Wombeyan specimens (for example, the P^1 close to P^3, and the molar cusps well developed) are what one would expect in specimens of somewhat young individuals. A modern specimen from New South Wales (AM, M3006) has the P^1 placed as in P4196, and another (AM, M4099) has molar cusps precisely as in P4196.

P4196 (Pl. 3, fig. 7, this paper) is here nominated LECTOTYPE of *Pseudocheirus antiquus*, and F51881 and its features are excluded from the diagnosis.

Pseudocheirus antiquus should be placed in the synonymy of *Pseudocheirus peregrinus*.

Burramys parvus Broom

This name remains valid for the species.

Potorous tridactylus var. antiquus Broom

AM specimens F4201 (maxilla) and F51880 (dentary) are two of the syntypes of *Potorous tridactylus* var. *antiquus* and teeth of these were illustrated in Plate VI (Figs. 4 and 6, and 7, respectively) of the original diagnosis (Broom 1896c). Broom distinguished the 'var. *antiquus*' on the basis of the short P^4 with four grooves. The number of grooves is variable within populations of the species, however.

The shape of the P^4 of F4201 indicates that it is *P. tridactylus* rather than *P. apicalis*, but its length ($6\cdot3$ mm) and the P_4 length in F51880 ($5\cdot2$) are 15 and 17 per cent less than corresponding means in a modern south-eastern Australian series of *P. tridactylus* ($p = 0\cdot040, 0\cdot038$). Dimensions of other teeth (dP^4, M^1) of the Wombeyan specimens are 5-10 per cent less than for modern *P. tridactylus* but the differences are not significant.

F4201 (Pl. 3, fig. 5, this paper) is here nominated LECTOTYPE of *Potorous tridactylus* var. *antiquus*, and F51880 (Pl. 3, fig. 6) remains as a PARATYPE.

P. tridactylus gilberti of Western Australia has premolars short as in the Wombeyan specimens, and considerable intraspecific variation is found in other potoroine macropodids from fossil deposits, for example, *Bettongia lesueur* (Wakefield 1964). Pending study and understanding of these matters, the Wombeyan *antiquus* cannot justifiably be distinguished taxonomically from *P. tridactylus tridactylus*.

Macropus wombeyensis Broom

AM, F4199 (dentary) is one of several syntypes of *Macropus wombeyensis*, and details of it comprise Figs. 2 and 3 of Plate VI of the diagnosis (Broom 1896c). Other syntypes have not been available for examination, but Broom's measurements of them are similar to those of F4199.

The available specimen is closely similar to modern examples of *Wallabia bicolor* from eastern New South Wales. For example, length of P^4, of M^{1-3} (crown), and the crown length of the toothrow (P^4-M^4), are $7\cdot0$, $21\cdot2$ and $38\cdot1$ mm in F4199, and $7\cdot0$, $21\cdot9$ and $37\cdot8$ in M5222 (AM) from Wyong.

F4199 (Pl. 3, fig. 9, this paper) is here nominated LECTOTYPE of *Macropus wombeyensis*. The name should be placed in the synonymy of *Wallabia bicolor*.

Mastacomys wombeyensis Ride

The species was distinguished (Ride 1956b) on the basis of a single maxilla (AM, F42322) having an additional small cusp on the M^3 and a proportionately 'wide' (i.e. long) zygomatic plate. Two further specimens from the Wombeyan Caves breccia are identified as *M. wombeyensis* by Schram and Turnbull (1970), each with the additional cusp more or less developed.

In a review of the taxonomy of *Mastacomys* (Wakefield 1972), *M. wombeyensis* is placed in the synonymy of *M. fuscus*. This conclusion is supported by a series of 20 maxillary specimens from the Wombeyan Caves quarry deposit, only two of which possess the auxiliary cusp.

AGE OF WOMBEYAN FOSSIL FAUNA

Wombeyan Caves is situated at 2,000 ft elevation, 4 miles on the seaward side of the Great Dividing Range, eastern New South Wales, in an area of Silurian limestone approximately 2 miles long and ½ mile wide, in a general region of granitic rock (Carne and Jones 1919).

The few annual rainfall figures for Wombeyan Caves correspond closely to those for the same years at Taralga, 11 miles distant, so Taralga's mean of 30·5 in. per annum for a 73-year period may be taken to approximate closely to that for Wombeyan Caves for the same period. This figure is close to the mean for Buchan (32·1 in.) over about the same period (78 years in this case), and would approximate also to the mean for the Pyramids area.

The site of the Wombeyan deposit is in a slight depression on a ridge overlooking the valley of Wombeyan Creek (Pl. 2). It is approximately 30 chains (600 m) from the edge of the acid rock across the valley, and only 10 chains (200 m) from a tongue of acid rock in the other direction. The vegetational formation on the limestone is woodland, with *Eucalyptus melliodora* dominant and shrub thickets about the actual rock outcrops. The granitic formation carries dry sclerophyll forest. Before it was cleared, the small creek valley below the Wombeyan site would have carried elements of warm-temperate rainforest.

Distributional data presented by Marlow (1958) show that the modern small marsupial fauna of the southern part of the Blue Mountains, where Wombeyan is situated, is very similar in species composition to that of eastern Victoria (see pp. 2-6).

Thus there is very close similarity in geology, topography, climate, vegetation and modern mammal fauna, between the Pyramids and Wombeyan Caves areas, and it may be expected that contemporaneous faunas and vegetational formations in the two areas would have been very similar in the past.

Ride (1960) concluded that owls were mainly responsible for the Wombeyan deposit, and similarity to the Pyramids deposit, both in species composition and maximum size of individuals, indicates that the same species of owl, or species of very similar habits, were responsible for the two deposits. Because of the similar sampling process, the age of the Wombeyan Caves breccia deposit may be considered in the light of data and hypotheses applying to the Pyramids deposit. Relevant points are:

1. *Cercartetus lepidus* and *Pseudomys higginsi* occur in the Wombeyan breccia and in the older fraction of the Pyramids deposit. Neither species is recorded either as a modern living animal on the Australian mainland or in any mainland fossil deposit representing a modern-type faunal assemblage.

2. *Burramys parvus* and *Gymnobelideus leadbeateri*, existing today only as relict populations, appear in the Wombeyan deposit and in the older Pyramids fraction.

3. The Wombeyan Caves quarry deposit (Hope 1971) contained fossils of large Pleistocene species (*Zygomaturus, Sthenurus, Palorchestes, Sarcophilus laniarius*) associated with elements of the small-mammal fauna of the Broom breccia (*Burramys parvus, Pseudomys higginsi* and others).

4. *Rattus fuscipes assimilis, Acrobates pygmaeus* and *Antechinus stuartii*, the three most abundant mammals in the older Pyramids fraction, are rare or absent in the Wombeyan breccia deposit. Each is widespread in south-eastern Australia and each is an index of wet forest conditions (see pp. 3, 5).

5. *Phascogale tapoatafa, Cercartetus nanus, Pseudomys higginsi, Pseudomys fumeus* and *Mastacomys fuscus*, each present in the Wombeyan breccia, increased in relative abundance in the older Pyramids fraction when, according to evidence from the colour analysis (p. 12), conditions were becoming less wet. Of these species, *Pseudomys fumeus* is the most abundant and *Cercartetus nanus* is second in abundance, in the Wombeyan sample listed by Ride (1960), and these two are similarly placed in the analysis of the deposit from the comparatively dry Victoria Range habitat (Wakefield 1963b).

6. *Pseudomys oralis,* present in the Wombeyan deposit and the most abundant mammal in the younger Pyramids fraction, is absent from the older Pyramids fraction. *Antechinus flavipes*, whose south-eastern Australian habitats are dry sclerophyll forest and woodland (Wakefield and Warneke 1967), and *Sminthopsis murina* of similar ecology, were present in the Wombeyan breccia deposit and absent from the whole of the Pyramids deposit.

7. *Burramys parvus* and *Gymnobelideus leadbeateri*, present in the Wombeyan breccia, reached their highest percentages in category 6 of the older Pyramids fraction, immediately preceding

TABLE 4

Location and Precipitation Data of Places Mentioned in Text

Location	Lat. S	Long. E	Precip. ins.	Location	Lat. S	Long. E	Precip. ins.
Bacchus Marsh	37°41'	144°27'	20.0	Mount Hamilton	37°47'	143°00'	21*
Bairnsdale	37°50'	147°38'	27.1	Mount Hotham	36°58'	147°08'	58.5
Basin Creek (head)	37°36'	148°15'	40*	Mount St. Bernard	37°00'	147°05'	58*
Bass River	38°29'	145°27'	41*	Murray-Darling Jn.	34°07'	141°55'	10*
Beech Forest	38°38'	143°34'	67.6	Murrindal River	37°25'	148°12'	34*
Bega	36°40'	149°50'	34.5	Nagiloc	34°28'	142°21'	11*
Bendock	37°09'	148°53'	27.8	Narracan	38°15'	146°14'	41.6
Bete Bolong	37°34'	148°19'	33*	Nelson	38°04'	141°01'	28.9
Brit Brit	37°27'	141°46'	24*	Nowa Nowa	37°44'	148°05'	31*
Broadford	37°13'	145°03'	24.5	Orbost	37°42'	148°27'	33.0
Buchan	37°30'	148°10'	32.1	Otway Ranges	38°40'	143°30'	
Carisbrook	37°02'	143°49'	20*	Ouyen	35°04'	142°20'	13.0
Cashmore	38°19'	141°29'	32*	Pomonal	37°12'	142°37'	28.2
Casterton	37°35'	141°24'	24.5	Portland	38°21'	142°36'	35.7
Cavendish	37°31'	142°02'	25.8	Pyramids	37°27'	148°12'	33*
Colbinabbin	36°35'	144°49'	18.9	Shepparton	36°23'	145°25'	19.9
Dadswells Bridge	36°55'	142°31'	20.0	Silverband Falls	37°11'	142°31'	36*
Falls Creek	36°52'	147°17'	94.4	Stoneyford	38°20'	143°20'	28*
Ferny Creek	37°52'	145°21'	50*	Stradbroke Island	27°30'	153°30'	
Forrest	38°31'	143°43'	40.3	Sunnyside	36°48'	147°30'	40*
French Island	38°21'	145°21'	33.8	Tanjil Bren	37°50'	146°12'	68.5
Gelantipy	37°11'	148°16'	36.3	Taralga	34°24'	149°49'	30.5
Gellibrand River	38°32'	143°32'	42.7	The Basin	37°27'	148°17'	33*
Gorae	38°14'	141°33'	33*	Thomson River, upper	37°46'	146°10'	75.7
Grampians	37°30'	142°15'		Tolmie	36°56'	146°14'	32.9
Halls Gap	37°08'	142°32'	36.0	Toolangi	37°33'	145°29'	50*
Hastings River	31°30'	152°30'		Tyabb	38°16'	145°11'	33*
Healesville	37°40'	145°31'	40.2	Victoria Range	37°23'	142°14'	
Heathmere	38°14'	141°38'	32*	Waratah Bay	38°48'	146°06'	40*
Hordern Vale	38°46'	143°31'	44.4	Warburton	37°46'	145°41'	52.9
Kangaroo Island	35°40'	137°20'		Warrenbayne	36°41'	145°53'	28.9
Kallista	37°52'	145°32'	54.8	Warrnambool	38°23'	142°29'	27.8
Kaniva	36°23'	141°15'	18.0	Wilson's Promontory	39°00'	146°25'	40.8
Kew	37°49'	145°02'	26*	Wombeyan Caves	34°19'	149°59'	30*
Loch Valley	37°47'	146°01'	56*	W Tree	37°20'	148°15'	36*
Marysville	37°31'	145°45'	54.8	Wyong	33°17'	151°25'	45.8
Mooroopna	36°24'	145°22'	19.2	Yalmy River	37°20'	148°30'	40*
Mount Dandenong	37°49'	145°21'	57.9	Yellingbo	37°49'	145°31'	37*

Note: Location of features such as mountains and streams is indicated at approximately centre of feature. Precise precipitation (inches, mean annual) is given when this has been available from the Bureau of Meteorology, Melbourne. Figures with asterisk are estimates based on data of adjacent towns.

the dry habitat assemblage of category 5 (see p. 22).

Points 1-3 indicate that the Wombeyan breccia deposit and the older Pyramids fraction represent the same small-mammal fauna, the fragmentation of which was probably associated with the extinction of large Pleistocene marsupials (see p. 17). Points 4-7 strongly suggest that the Wombeyan breccia deposit is about the same age as the final stages of accumulation of the older Pyramids fraction.

Broom (1896) assessed the Wombeyan breccia fauna as 'later Tertiary', and he believed it to contain extinct species and species ancestral to modern ones (Broom 1896a, 1896b). The present study indicates that the breccia deposit contains no wholly prehistoric species, and that its small mammals are in no cases very different from modern ones (see pp. 19-20).

The summaries, pages 17 to 20, show that in morphological characters the Wombeyan breccia fauna and the Pleistocene Pyramids fauna each exhibit about the same amount of variation in comparisons with the Holocene and modern faunas. In each of the first two assemblages the majority of species do not differ significantly from those of the Holocene or modern assemblages. Two species (*Potorous tridactylus* and *Pseudocheirus peregrinus*) of the Wombeyan fauna, and two (*Perameles nasuta* and *Schoinobates volans*) of the Pleistocene Pyramids fauna, differ in tooth-size from corresponding Holocene or modern series. In proportions, variation from Holocene or modern series occur in the Wombeyan *Pseudomys oralis* (in incisive foramina) and two Pleistocene Pyramids species: *Antechinus swainsonii* (in ascending processes of dentary) and *Rattus fuscipes* (in zygomatic plate). Both the Wombeyan and the Pleistocene Pyramids *Mastacomys fuscus* have smaller teeth and longer zygomatic plate than in the Holocene and modern series from the Australian mainland. These analogies add weight to the suggestion that the Wombeyan breccia deposit and the older fraction of the Pyramids deposit are of similar antiquity.

For the Wombeyan breccia fauna Ride (1960) suggested 'an age somewhat later than the last pluvial period of the Pleistocene'. Lane and Richards (1967) state that this suggested age 'appears to be too recent to be consistent with the topography'.

It is probable that the Wombeyan deposit accumulated on the floor of a recess similar in character to the outer chamber of the Pyramids Cave, in a small cliff or steep limestone outcrop (see Plate 2). The 'two teeth . . . but no bones' of *Thylacinus*, and the *Wallabia* jawbones, found in the Wombeyan deposit (Broom 1896c), and the absence of other remains of large animals, is remarkably similar to the occurrence of a single tooth of *Sarcophilus* and fragmentary macropodid remains in the Pyramids Cave (see p. 7). This indicates that the Wombeyan recess was used as a den by *Thylacinus* and that it took parts of its wallaby victims there. Owls would have needed a sheltered ledge in the recess, out of reach of terrestrial predators. There is now no evidence of a cliff line or of a steep slope at the actual site, but it is not unlikely that, being on an exposed hill, an outcrop containing a recess should have weathered to the present topography in several thousand years.

The available data suggest an age of the order of 10,000 years for the Wombeyan Caves breccia deposit.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATES

PLATE 1

Details of Pyramids Cave

FIG. 1—Limestone cliff, eastern side of Pyramids hill, with openings of outer chamber and lower tunnel of cave indicated by arrows. The large shrub below the outer chamber is *Pittosporum undulatum* and the tree crown in the foreground is of *Eucalyptus melliodora*.

FIG. 2—View from within outer chamber, with owls' landing platform low in foreground. The background is dry sclerophyll forest across Murrindal River.

FIG. 3—Tooth (I_3) of *Sarcophilus laniarius* (arrowed), and sample pieces of fragmented bones presumably of prey of *Sarcophilus*; × 1·4.

PLATE 2

Bone breccia site, Wombeyan Caves

FIG. 1—The general environs: the 'cave' is between the figures. The tree on left is *Eucalyptus melliodora*.

FIG. 2—The 'cave'. The breccia was obtained from the floor of the depression.

PLATE 3

(All figures × 3.)

Fossil specimens described by R. Broom, from Wombeyan Caves deposit

FIG. 1—AM, F4198. Lectotype of *Perameles wombeyensis* Broom (= *Isoodon macrourus*). Part dentary, with M_2.

FIG. 2—AM, F51878. Syntype of *Perameles wombeyensis* Broom, now excluded from diagnosis (= *Perameles nasuta*). Part dentary.

FIG. 3—AM, F17501. Lectotype of *Palaeopetaurus elegans* Broom (= *Gymnobelideus leadbeateri*). Dentary with I, P_4 and M_1.

FIG. 4—AM, F51879. Syntype of *Perameles wombeyensis* Broom, now excluded from diagnosis (= *Perameles nasuta*). Part dentary, with C, P_1, P_3 and unerupted P_4.

FIG. 5—AM, F4201. Lectotype of *Potorous tridactylus* var. *antiquus* Broom. Cranial piece, with P^1 (unerupted), dP^4, M^1 and M^2.

FIG. 6—AM, F51880. Paratype of *Potorous tridactylus* var. *antiquus* Broom. Part dentary, with P_4 and bases of M_1 and M_2.

FIG. 7—AM, F4196. Lectotype of *Pseudocheirus antiquus* Broom (= *Pseudocheirus peregrinus*). Cranial piece, with P^3, P^4, incomplete M^1, and M^2.

FIG. 8—AM, F51881. Syntype of *Pseudocheirus antiquus* Broom, now excluded from diagnosis (= *Schoinobates volans*). Part dentary, with diagnostic short angle (at lower right).

FIG. 9—AM, F42322. Lectotype of *Macropus wombeyensis* Broom (= *Wallabia bicolor*). Part dentary, with P_4 (left), M_4 (right), and the intervening molars (M_1, M_2, M_3) somewhat broken away.